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BRITISH GRAHAM LAND EXPEDITION

1934-37



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BRITISH MUSEUM (NATURAL HISTORY)

BRITISH GRAHAM LAND
EXPEDITION, 1934-37

SCIENTIFIC REPORTS

Volume I, Nos. 1-9

LONDON

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INTRODUCTION

THE British Graham Land Expedition, 1934–37, under the leadership of Mr. John Rymill, an Australian, was the first full-scale British Expedition to winter in the Antarctic since Shackleton's men returned in 1916. It was mainly financed from funds at the disposal of the Colonial Office. In addition, it received substantial monetary help from the Royal Geographical Society and many private benefactors, chief amongst whom was Lord Wakefield.

The Expedition sailed in the three-masted topsail schooner, R.Y. *Penola*, of 150 tons nett, which was manned entirely by the members of the Expedition, who were all volunteers. The following in brief is the story of their travels. On 10 September, 1934, the *Penola* sailed from the Thames; a fortnight later she touched at Madeira and reached the Falkland Islands at the beginning of December. Port Stanley was left at the new year and the Argentine Islands on the west coast of Graham Land were finally reached on 14 February, 1935, after considerable trouble with the ship's engines, troubles which had far-reaching effects on the *Penola's* subsequent capabilities. At the Argentine Islands a base was established and there too the ship wintered.

Owing to poor winter ice conditions work during that first year was limited, apart from flights by a small Fox Moth aeroplane, to the islands and mainland coast within a hundred miles of the base. Then, in January 1936 the *Penola*, with the ship's party on board, visited Deception Island. Her next task was to transport the whole Expedition in mid-February to the Debenham Islands in Marguerite Bay where a new base was erected. Here the shore party was left while the ship sailed north to the Falklands and South Georgia for a refit.

The main geographical work of the Expedition was carried out from this southern base between March 1936, and February 1937. The chief result of this part of the work was the proof of the peninsularity of Graham Land and the discovery of King George VI Sound.

The *Penola* returned to Marguerite Bay in February 1937, and the whole Expedition sailed for home.

A general narrative of the Expedition has been provided by its leader in his *Southern Lights*, published by Chatto & Windus in 1938.

The following list contains the names of the members of the Expedition and their chief jobs.

LIST OF MEMBERS

(In alphabetical order, with rank at time of Expedition).

J. R. Rymill	Leader.
G. C. L. Bertram	Biologist.
E. W. Bingham	Doctor, Surgeon-Lieutenant-Commander, R.N.

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V. D. Carse	Ship's Party.
W. L. S. Fleming	Chaplain and Geologist.
N. A. Gurney	Ship's party.
W. E. Hampton	Second-in-command and Pilot.
J. H. Martin	Mate
I. F. Meiklejohn	Wireless Operator, Lieutenant, Royal Corps of Signals.
H. M. Millett	Chief Engineer, Lieutenant-Commander (E.), R.N.
J. I. Moore	Second Engineer.
Q. T. P. M. Riley	Second Meteorologist.
B. B. Roberts	Ornithologist.
L. C. D. Ryder	Second Mate, Captain, Royal Norfolk Regiment.
R. E. D. Ryder	Captain. Lieutenant, R.N.
A. Stephenson	Surveyor and Meteorologist.

Throughout the Expedition the dominant aim was geographical survey, and the other sciences had to give precedence to it, a fact that naturally often resulted in breaks in continuity and other obvious troubles. The maps resulting from the Expedition's surveys have in the main already been published in the *Geographical Journal*. Among these is a general map (*Geographical Journal*, May, 1938), which includes all the surveys carried out by the Expedition, and the names of all the important localities mentioned in the biological reports. It was intended to reproduce this map here, by courtesy of the Royal Geographical Society, but unfortunately, the destruction of the lithographic stones by enemy action has made this no longer possible.

All the biological collections made by the Expedition have been presented to the Museum. Chief among these are the large collections of seal skulls and bird skins. This first volume of the Expedition's results includes Reports on the major part of the biological work.

MARTIN A. C. HINTON

(Keeper of the Zoological Department)

June, 1941

BRITISH MUSEUM (NATURAL HISTORY)

BRITISH GRAHAM LAND EXPEDITION

1934-37

SCIENTIFIC REPORTS

Volume I, No. 1, pp. 1-139

*THE BIOLOGY OF THE
WEDDELL AND CRABEATER SEALS*

*WITH A STUDY OF THE
COMPARATIVE BEHAVIOUR OF THE
PINNIPEDIA*

By

G. C. L. BERTRAM, M.A., Ph.D.

Zoological Laboratory, Cambridge

WITH TEN PLATES AND FORTY-TWO TEXT FIGURES

LONDON

PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

THE BIOLOGY OF THE WEDDELL AND CRABEATER SEALS :

WITH A STUDY OF THE COMPARATIVE BEHAVIOUR OF THE PINNIPEDIA

By G. C. L. BERTRAM, M.A., Ph.D.
Zoological Laboratory, Cambridge

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INTRODUCTION

THE field work which formed the basis of the present paper was carried out in the course of the British Graham Land Expedition 1934-37. This Expedition was primarily engaged in survey work on the west coast of Graham Land, in the Falkland Islands Dependencies, Antarctica. From January 1935 until February 1936 the work was carried out from a base at the Argentine Islands in $65^{\circ} 15' \text{ S.}$ and $64^{\circ} 16' \text{ W.}$ In the following year, from February 1936 until March 1937, the Expedition was based upon the Debenham Islands in $68^{\circ} 08' \text{ S.}$ and $67^{\circ} 06' \text{ W.}$

During the course of the Expedition it was necessary to kill a total of 558 seals to provide food for 16 men and an average of some 80 dogs. Of these seals 367 were Weddells, 177 Crabeaters, and 14 Leopards, and the observations that the author was able to make on these animals form the main basis of the present paper. No Ross seals were seen. To a large extent the leader of the Expedition put the killing of seals into the author's hands to enable him the more easily to do his biological work. The author took every opportunity of doing the actual killing and butchering himself, for only in that way was it possible to obtain all the desired details from each carcase. Even so, examination frequently had to be extremely hurried or omitted for obvious reasons of expediency, weather, and locality. So far as possible the seals were shot in the neck in order to leave the skulls undamaged. Unfortunately all too often the opportunity of getting in a large supply of meat coincided with periods when the facilities for examination and preservation of material were at their worst. Thus it was sometimes possible to preserve the ovaries of certain seals but not their skulls, while in other instances the reverse only was possible. To a large extent this was unavoidable, but often the disadvantages of circumstance could partly be overcome by ingenuity and experience.

ACKNOWLEDGMENTS

I have much pleasure in thanking all those who helped me in the collection of the material and in its later study. In the first place I should like to thank my

fellow-members of the British Graham Land Expedition 1934–37 for their help in the field, and especially the ship's party during the year at the Argentine Islands. To Brian Roberts, ornithologist to the Expedition, I am particularly grateful for his suggestions and encouragement both in Antarctica and in Cambridge. I also owe a particular debt of gratitude to Dr. Alton A. Lindsey, of the second Byrd Antarctic Expedition, for access to certain of his original notes, and to Dr. N. A. Mackintosh and Mr. J. E. Hamilton for their suggestions and advice. Further, I have pleasure in thanking Messrs. J. A. F. Fozzard and S. J. R. Reynolds for their skill in X-ray photography.

The work on the material in England, from 1937–39, was carried out at the Zoological Laboratory, Cambridge, while in receipt of a grant from the Department of Scientific and Industrial Research.

PRESENTATION

This paper on the Weddell and Crabeater seals (*Leptonychotes weddelli* and *Lobodon carcinophagus*) describes the biology of the two most abundant of the four species of Antarctic Phocids, the other two species being the Leopard seal (*Hydrurga leptonyx*) and the Ross seal (*Ommatophoca rossi*). It has been found most convenient to treat the Weddell seal first, since of that species there is most knowledge, then to describe the Crabeater seal, comparing and contrasting it with the foregoing description of the Weddell. For each species, 'special habits and attributes', 'reproduction' and 'growth and age' are described in turn, and followed by a short statement of the composition of the population of the species, so far as it can be determined from the evidence available. These descriptions of the two species are followed by a more general discussion of certain points of behaviour among the Pinnipedia as a whole.

In the present instance very little use is made of the previous collections of Weddell and Crabeater material from the Antarctic. The skulls in the British Museum (Natural History) have been examined and measured, but in comparison with the present series the numbers available are small, in most instances the data are inadequate, and the geographical origin is widespread. For these reasons the skulls in the national collection are of little help in interpreting the finer details of the bionomics of the Weddell and Crabeater seals.

THE WEDDELL SEAL

Leptonychotes weddelli (Lesson)

INTRODUCTORY

PREVIOUS KNOWLEDGE OF THE SPECIES

The synonymy has been adequately dealt with by Allen (1905) and Wilson (1907). The first notice of the Weddell seal appeared in 1822 as a short description by Professor Jameson in Weddell's *Voyage towards the South Pole* (1825). It was first

described with any adequacy by Lesson (1826). Until 1900 it was still one of the least known of described mammals owing to the inaccessible nature of its habitat. Barrett-Hamilton (1901, 1902) then described the collections brought back by the *Belgica* and *Southern Cross* Expeditions from Graham Land and South Victoria Land respectively, and Wilson (1902) added some supplementary notes. Allen (1905) provides a full bibliography of the earlier knowledge of the species.

The first detailed account of the life-history and habits of the species is due to Wilson (1907), as a result of his work with the National Antarctic Expedition 1901–4. Other papers dealing with particular aspects of the species are those of Turner (1888), Hepburn (1915), and Haig (1915) on the anatomy, and Tims (1910) on the embryology. After Wilson's report, which was completed in 1907, no further detailed account of the general biology of the species based on new work appeared for 30 years, when a short but detailed paper was published by Lindsey (1937). On the first page of his paper Lindsey remarks: "During the first Byrd Antarctic Expedition, P. A. Siple recognized the desirability of an intensive study of the Weddell seal, and he initiated such a project in the summer of 1929–1930 in the Bay of Whales. During the second Byrd Expedition, the summer of 1934–1935 was devoted by the present writer [i.e. Lindsey] largely, and the preceding 8 months in part, to this work." Lindsey in particular was able to do very valuable work on the growth of the pups, a work that must have been most trying in its execution. The extent to which the present author is indebted to the writings of Wilson and Lindsey is apparent from the quotations made from their excellent papers.

As a member of the British Graham Land Expedition 1934–37, the present writer was at work in the Antarctic from January 1935 until March 1937, and during that time his major biological work was the study of the seals of the west coast of Graham Land. Thus Lindsey's work in the Ross Sea ceased a month or two after the present writer's work started in West Antarctica. Each was unaware of the work of the other until after the publication of Lindsey's paper in May 1937, which coincided with the return of the present writer to England.

DISTRIBUTION OF THE WEDDELL SEAL

The Weddell seal is circumpolar, and its normal habitat is the inshore waters of the Antarctic continent and adjacent islands. It spends much time in the water, but emerges at intervals to lie out on the beaches or on fast-ice. It is not a seal of the Antarctic pack-ice and is rarely found on isolated floes or far from land. Beyond the South Shetlands, it is abundant at the South Orkneys, and is also found at the South Sandwich Islands, and there is a small permanent colony in Drygalski Fjord, South Georgia (Matthews, 1929). It has been found at most of the other subantarctic islands, and is probably a regular inhabitant of some of them in small numbers. There are records of the animal being found still farther afield, for example, at the Falkland Islands. Wilson (1907, pp. 12–13) remarks "It has been reported from Juan Fernandez, Kerguelen and Heard Islands, and even from New Zealand . . . The first specimens placed in the British Museum were procured from the River Santa Cruz on the east coast of Patagonia," by Captain Fitzroy in 1833. That the Weddell

seal is sometimes seen on the coast of New Zealand is confirmed by R. A. Falla (private communication).

The Weddell seal is the most southerly ranging mammal, apart from man himself, and is the seal most specialized for life in high latitudes, where so much of the year must be spent beneath the ice.

INTRODUCTORY DESCRIPTION OF LIFE AND HABITS

The Weddell seal is semi-gregarious, this habit appearing to be more the result of living in the same area than of an innate love of its fellows. The adult Weddell seal feeds on fish and Cephalopods, and may grow to a length of a little more than 9 ft. from nose to tail. The colour of the animal is dark, almost black above, more or less flecked and striped with splotches of white laterally and ventrally. There is an annual moult in the summer months. The adult animals spend long periods lying out on floes or fast-ice, or on open beaches where such exist. On land they are in no way timid and may be closely approached. Out of water they are sluggish, in the water active and swift swimmers. The fore-limbs are of even smaller size than in most other Phocids, and do not even touch the ground in progression on land.

The winter is spent under the ice, breathing holes being kept open for the purpose. The females emerge very early in the antarctic spring to give birth each to a single pup on the ice, the adults at this time often collecting together into large or small groups. Gestation is about 10 months. The seals in the same area pup almost simultaneously, the limit of the pupping season being a little over one month, with a distinct peak within that period. The pups are about 4 ft. long at birth, weigh some 60 lb. and possess a thick woolly coat quite unlike that of the adults. Growth proceeds rapidly. Moulting of the woolly coat starts at about a fortnight old and is complete in about another 4 weeks. Permanent separation from the mother takes place about a week later, by which time lactation has ended. At first the young seals subsist largely on Crustacea, but the adult diet is soon acquired. Growth continues to be rapid, and when the young females are 26 months old they become pregnant for the first time. Each female normally pups at the end of her third and each succeeding year, but probably few live to pup as many as six times.

SPECIAL HABITS AND ATTRIBUTES

Food

In the section on lactation details are given of the age at which the pups begin to feed for themselves. The normal age at weaning seems to be about 7 weeks, (Lindsey, 1937), and the pups then pass through a transition period when they subsist largely upon Crustacea, before assuming the adult diet. The Harp seal (*Phoca groenlandica*) apparently has a similar transitional diet (Hjort and Knipowitsch, 1907; Nansen, 1925). When adult the Weddell seal feeds almost exclusively on fish and Cephalopods. Off the west coast of Graham Land these constituents are about equally represented in the stomachs. In the Ross Sea area one gathers from Wilson's

(1907) and Lindsey's (1937) descriptions that the proportion of Cephalopods is much lower. Probably the adult Weddell seal takes fish and Cephalopods impartially according to whichever is the more convenient or abundant. In the adult Weddell stomachs Euphausiids are found but rarely; rather more frequent are Amphipods and Isopods, which have probably been obtained from the bottom rather than in mid-water. In some cases Crustacea found in Weddell stomachs have clearly been swallowed along with the fish that had already devoured them so tending to give a wrong impression as to the seal's real diet. Other food substances are very rare. In one instance a number of large, dark-brown Holothurians about 1 ft. long were found to have been eaten, these beasts being common in the shallow water on rock bottoms in certain places along the Graham Land coast.

The depth at which the fish and Cephalopods are obtained is not known. Often the seals are living in quite shallow water, but when there is a much greater depth one imagines that food-catching is limited to the upper layers, though it is known that seals can dive on occasion to considerable depths. The fish eaten may be as much as 18 in. in length, but 9 in. is more nearly the average size. The various species of Nototheniids, by far the most abundant group of antarctic fishes, form the main supply. Of the Cephalopods eaten by the Weddell seal, none were obtained in Graham Land in sufficiently fresh condition to make certain identification possible. That the remains were truly those of Cephalopods there could be no doubt whatever. These Cephalopods possessed no hard calcareous internal skeleton. The largest of them had beaks which were sometimes as much as $1\frac{1}{2}$ in. long. The numbers of squids were often enough to leave after digestion a residue in the stomach that appeared almost like a fine gravel, composed entirely of the fragmented beaks. Doubtless such a collection might be cumulative, but a pint of this residue in a single seal must indicate the abundance of Cephalopods in the area.

The amount of food eaten by a Weddell seal is difficult to determine. The stomach of an adult when full contains about 16 lb. of fish and squids. From the long periods that the individual seals seem to spend lying out at the same spot, one would judge that probably they do not fill their stomachs to this extent more than perhaps once in every 2 or 3 days. On this estimate each adult seal consumes about 1 ton of fish and squids in the course of a year, which represents about three times its own body weight. Compared with many animals this is a small ratio between food and body weight, doubtless connected both with the good insulating properties of its blubber layer, once attained, and the creature's rather sluggish habits.

Reliance cannot, however, be put on the above statements, since the observations have for the most part been made in the moulting season, when feeding may well be less frequent than normally. It was evident that of the animals lying out at any one time, those with relatively empty stomachs were far more active when approached than those in which the stomach was full of freshly-caught food.

SWIMMING AND DIVING

The pups of the Weddell seal take to the water at a very early stage. Lindsey (1937, p. 139) states that they "do not postpone entering the water until after completing the moult, but are to be found swimming at frequent intervals throughout

this period. In fact, two pups took to the water at 8 and 9 days of age, before the moult had begun. One was observed swimming at 10 days, another at 14, four at 16, and seven more before 20 days." It is a little difficult to feel confident that these very early records of swimming by the pups were not due in part to the disturbance caused by the presence of men. The female Weddells with pup vary greatly in their reactions to the approach of men, some attaining almost to fierceness, other being passively indifferent, while a few are more timid than at normal times. Such variations may in part account for the differences in age at which the pups have been observed to take to the water, but it seems clear that the pups suffer in no immediate way from the early introduction to the adult environment. From the beginning the pup "can float with its nose above the surface, even when apparently it is perfectly motionless. Occasionally the female supports it with her body, more from playfulness than necessity. Often she pushes its head under, although the pup frequently submerges of its own accord. . . . At about 25 days the pup may swim alone between holes . . . [but] a pup at 34 days still hesitated to enter the water, although it had been seen swimming 12 days previously. After it had tentatively thrust in its head several times, the adult tugged it in by the scruff of the neck. A 48-day pup fully visible in open water kept submerged for a maximum duration of 167 seconds." Thus, in its ability to swim and dive the pup as soon becomes proficient as it does in the other adult attributes.

The speed of the adult in the water is doubtless variable and at all times is difficult to judge. From watching Weddells swimming through a narrow creek and comparing their speed with that of a motor-boat, it was judged that the 'normal cruising speed' of the animal is in the neighbourhood of 7 knots. Doubtless when necessary the animal can go a great deal faster. In normal swimming the hind limbs are used in the manner of a fish's tail, the palmar surfaces being opposed to one another and the digits spread widely apart, so stretching the web to the full. Swimming is by lateral undulations, rather than those in the vertical plane, as in the propulsive effort of the tails of Cetacea and Sirenia. In swimming the Weddell seal seems to keep the fore flippers closely pressed against the sides of the body at all times.

Little is known of the maximum lengths and depths of seals' dives. The timing of seals' dives in the natural state is very difficult and unreliable. Eskimos and others who have hunted in Greenland believe that the adult Bearded and Hooded seals (*Erignathus barbatus* and *Cystophora cristata*) can stay submerged for a quarter of an hour or even more. This may be so, but there is a tendency among waiting hunters to over-estimate time.

The depth to which seals will normally descend it is impossible to discover except by chance in particular instances. Nansen (1925) speaks of Harp seals being caught in nets set at a depth of 100 fathoms, but it is difficult in such instances to preclude the possibility of the animals having been enmeshed during the nets' passage to the surface. A single circumstance came to the notice of the present writer that bears upon the subject. This was the finding of an adult male Weddell 95 in. long in a rift in the shelf ice of King George VI Sound in October 1936. The rift, situated about a dozen miles from the edge of the shelf-ice in the opening of the Sound, was quite isolated from other rifts and from tide cracks, and its walls were 40 to 50 ft. in

height. The seal was lying beside a small crack or hole in the sea-ice at the bottom of this narrow rift, which was itself about 25 ft. wide, for the most part with overhanging corniced edges. The question is, of course, whether the seal reached this point by making its way over the ice or by swimming beneath it; in the latter case we should have some indication of the depth to which it must have dived. The consistency of shelf-ice is such that it floats with roughly one-sixth of its bulk above water, and five-sixths beneath. In the present instance, where the ice cliffs above sea level were 40 to 50 ft. in height, this means that beneath the sea the rift was bounded by walls about 300 ft. (50 fathoms) in depth. If this male seal had reached the spot by the submarine route it must have dived to greater depths, quite apart from how this point of access to the air above was discovered. On the other hand the seal might have come the dozen or more miles over the ice and by chance have come upon this local access to the sea beneath. Quotations from Wilson (1907) are made in a later section on the subject of old male seals creeping away to die, and the animal here concerned may have been doing likewise. Its gut was quite empty except for a few small stones and some fish or squids' eye lenses in the stomach. The left hind flipper was damaged, the distal phalanges being exposed for several inches. Otherwise the seal seemed to be in good condition, with the blubber of normal thickness. If the animal came over the ice it was fortunate in finding the only rift in the area that had in its floor an open crack. Conclusions as to the diving powers of seals are dependent on such unsatisfactory evidence as this.

Scholander (private communication) in Norway is, however, at present actively engaged in the investigation of the physiology of diving in seals. His findings seem to show that both the lengths and depths of seals' dives can be greater than has usually been supposed. He finds that even quite young pups of the Hooded and Harp seals have remarkable diving power, but submarine ability improves with both age and experience. Irving *et al.* (1935, p. 150), after a study of the respiratory metabolism of the Common seal (*Phoca vitulina*) state that "the observed quantitative difference in respiratory, cardiac and vasomotor control is sufficient to indicate that the physiological adjustments of a diving animal may be only quantitative developments of the typical mammalian controls."

A further point that arises is how seals navigate beneath the ice and find the air holes. At certain times doubtless this is done simply by sight, a stronger light being visible to the seal at distant points where the ice is broken. The most difficult time one would imagine to be winter, when the ice covering the sea in bays and fjords is unbroken but for the tide cracks and holes kept open by the seals. For much of this time too there is darkness even above the ice, so that the amount of light penetrating into the water through a foot or two of ice, itself covered by several more feet of snow, must be negligible so far as ordinary sight is concerned. How then do the seals find their way about and return to the points of access to the air? Where there are cracks in the sea-ice (possibly the cracks caused by temperature changes are of great importance) breathing-holes may sometimes be found along them at intervals of 60 to 100 yds. But when the ice in a fjord or bay is quite unbroken so far as can be seen there are often intervals of, say, 700 yds. between the holes kept open by the seals themselves. Even during the darkest period of the year it is evident that the seals wander beneath the ice and do not stay continuously in the vicinity of the

breathing hole. If at such a time a new hole be cut in the ice, often within a few minutes a Weddell seal will come up and make use of it. Doubtless it is under the ice in the winter that the powers of submergence are tested to the full and, one would suspect, that the mortality is highest.

During the winter months the Weddell seals lie out on the ice to a very limited extent, the males, however, doing so more than the females. During this season it is much warmer beneath the ice than in the air, and the fact that in winter seals are usually found out only on the relatively calm days, suggests that this temperature difference may be a guiding factor in the habit. The seals are forced to make continual efforts to keep open the air holes, which tend to freeze up rapidly. This is done by frequent scraping with the canines and incisors, particularly of the upper jaw. This process has been adequately described by Wilson (1907) and Lindsey (1937). It seems doubtful whether during their time beneath the ice the seals can sleep. That they are capable of sleep in the water is seen occasionally in the open season, the animal floating at the surface, motionless but for raising the nostrils just clear of the water at intervals. This habit is much more common in the Elephant seal (*Mirounga leonina*), but in that species the back is more arched downwards so that the nose and tail remain clear of the surface. The Weddell seal in winter would seem to be in a state of enforced continual activity, feeding, breathing, and ice-sawing, except when favourable chance provides a vein of air beneath the ice, when perhaps the animal can for a time lie at the surface.

It is possible that under the ice in certain circumstances there are pockets of air and that the seal is able to make use of them. On one occasion in Graham Land two members of the Expedition were travelling over sea-ice of moderate thickness, and found that frequently when they prodded through the surface there was a small upward rush of air that had been trapped beneath the ice. Whether the air was actually present in sufficient quantity to be of use to seals is quite unknown, but the possibility of there being pockets of air should not be neglected in considering the winter habits of the Weddell seal.

MOULT

The moult of the Weddell seal was studied by both Wilson and Lindsey, the latter paying particular attention to it in the young animal. A series of quotations from these two authors gives a very fair picture of the process. Wilson (1907, p. 17), "At birth the young Weddell's seal is clothed in a woolly coat of long hair, of a rusty greyish colour, presenting but the faintest indications of any marking. . . . This woolly coat consists of two varieties of hair, the one 2·8 cms. long, fine and almost straight; the other shorter, fine and very curly, so curly, indeed, that in a hair 1·7 cms. in length there are no less than 8 or 10 curves or bends." Lindsey (1937, p. 138) takes on the story: "The moult from the natal wool of 22 individuals of known age began at from 9 days (in 5 cases) to 21 days of age, averaging 13·8 days. In one case the moult lasted only 18 days; in another it was not yet completed after 51 days' duration when the pup was 70 days old. The average duration of the moult is 30·2 days, so that at 44 days the average pup has replaced its woolly fur with a velvety black

and white coat of short hair identical with that of a freshly moulted adult. . . . The precise sequence of the first moult is quite varied, as is the rate of its progress in different individuals." Lindsey and Wilson both give an account of the precise sequence in which the various parts of the body moult. In general the woolly coat starts to drop out around the genital orifice and umbilicus, then the face is affected, then the flippers; soon patches appear on top of the head, and on the nape; later a collar round the neck, the head and the entire chest are moulted, while the dorsal side is 'still predominantly woolly'. "Loss of the remaining wool from the dorsal parts and flippers, and spreading of the ventral moult laterally, leaves only a slowly narrowing and thinning streak of wool along the sides as the typical final stage." (Lindsey, 1937, p. 138).

Wilson (1907, p. 24) states that the adult "Weddell's seal is to be found moulting at any time during the summer months. . . . Beginning in a line down the centre of the back from head to tail, the moult is almost simultaneous upon the head, upper neck, shoulders, fore and hind flippers. The old hair then begins to fall from the lower parts—neck, chest, and abdomen—while the last remnants of the old bleached hair are to be found on the sides of the body. . . . The change in colour thus brought about is often most remarkable. The old hair is a pale rusty-grey where it was once black or dark grey, and the spots and splashes of white and silver-grey, which appear in rich contrast with the black in the new coat, are disclosed by the falling of a rather dirty-looking whitish hair which is hardly whiter than the rusty-grey which covered up the black. Yet this seal never looks white in the weathered coat, as does *Lobodon*; rather it looks a dingy brown with inconspicuous markings." Some of the adult Weddells just prior to the moult in Graham Land (particularly some of those seen at Deception Island in January 1936) were almost of a uniform rusty-brown colour so that at first sight one scarcely recognized them.

The new coat is most handsome. Wilson (1907, p. 25) describes it as follows. "In the colouring of the adult Weddell's seal, perhaps the most typical characteristic is that the palest area is not ventral and median, but lateral or ventro-lateral. The dorsum is typically black; then comes a dorso-lateral area which is black with a few white streaks or splashes; then a lateral area in which the white blotches are larger and more abundant; then a ventro-lateral area in which the white is predominant, and very few darker markings are to be seen; and lastly, the median ventral area is grey with white spots and streaks or splashes. The tail is, dorsally, the blackest part of all, but has a narrow white border which is constant." There is, however, considerable variation, and some seals are very much darker or more spotted with white than the average here described.

In the Weddell seal feeding and other aquatic activities do not cease during the moult, though they may be diminished. This habit of the Weddell may be contrasted with that of the Elephant seal. Matthews (1929, p. 242) remarks: "When the seals are in the rookeries they do not feed. During the breeding season the cows and bulls fast for 2 months, and then, when the harems break up, they go to sea in December and return to land in January and February to change their coats. They stop ashore for another 6 weeks to 2 months and then return to the water and do not haul out again until the next breeding season. It must not be supposed, however, that all the seals arrive and depart with any regularity. . . ." It is not possible to

state at all precisely the time taken by the average Weddell seal to complete the moult. Probably it is variable. Matthews (1929, p. 242) states: "The process [in the Elephant seal] from the commencement of the shedding until the new coat is complete, lasts from a month to 5 or 6 weeks."

NOISES MADE BY WEDDELL SEALS

The Weddell seal is normally a very silent creature except in the breeding season, remaining mute until disturbed. Then the seal will "very likely make a little piping trill in his throat with his mouth shut," sounding "like the tinkling of water in a stone cistern" (Wilson, 1907, p. 12). If still more disturbed the seal may open its mouth wide and make a loud hissing noise by the forcible expulsion of the air in its lungs. At the breeding time the seals of both sexes are wont to make other noises, producing something of a roar that is so characteristic of the Pinnipeds as a group. "Weddell's seal when quite young gives a 'baah' like a sheep. This becomes a roar as the seal grows older, but other and more musical notes are common, such as a moan beginning with a high-pitched note and ending with a low one . . . or a series of plaintive piping notes may be produced, ending on the call note of a bullfinch, or changing to a long shrill whistle which terminates with a grunt or a snort or a gurgle." (Wilson, 1907, p. 12.)

The Weddell seal is not even completely silent under the ice in winter. Lindsey (1937, p. 143) remarks in this connection: "The calls given under water are of the types which are produced with the mouth closed; we often watched seals on the ice while they uttered the same sounds. One type is a series of deep guttural thumps, beginning rapidly but with gradually increasing intervals as it continues. Another consists of a series of very bird-like chirping notes, also diminishing in tempo. Other calls given above the ice with the mouth open, are loud bellowings, roars and moans, soft gurgling and grunting noises, and a staccato clicking together of the teeth. The pups give loud bleating and bawling cries." Lindsey goes on to state that "sound records of the various calls were made".

FIGHTING AND WOUNDS DERIVED THEREFROM

The amount of fighting among Weddell seals is not great, and is negligible in comparison with that which goes on among the males of the polygynous species. Among the females fighting scarcely occurs on a plane higher than that of chance snapping between individuals when concerned for the well-being of their pups. Lindsey (1937, p. 140) remarks: "Two females were seen to rear up and snap at each other's heads a few times, when one of them showed interest in another's pup. In December, two females were found on the ice a few yards apart, both bleeding badly as though from a recent fight. The eye of another had been put out. . . . One was wounded about the genital region, others on the breast, belly, or side. Possibly some such injuries are due to sharp edges of ice. The number of wounds and scars on the females is very small in comparison with those on males."

The period relative to copulation, at which the males are prone to fight, will become apparent in the discussion on the gestation period. Lindsey saw bulls, freshly wounded from fighting, as early as 15 October. (In the Bay of Whales, where his

observations were made in the seasons 1929 and 1934, the extreme dates of pupping were 5 October and 10 November, the median date being 23 October.) "No dead adults were found, although several bulls evidently were bleeding to death from fights with other seals, and were scarcely able to move." (*ibid.* p. 140). Such an end to a fight between members of the same species is probably rare. Lindsey goes on to remark, "No real fighting actually was seen; it probably occurs in the water, for the bulls emerge seemingly only to sleep on the ice. The injuries are inflicted chiefly about the genital orifice, head and neck, and are readily distinguishable from the long, deep gashes on the Crabeater seal caused by Orca. The cuts dealt by other seals are a few inches long. They suppurate freely and heal slowly. The skin of an aged bull presents a veritable network of black scars." Similar remarks apply to the seals observed by the present writer in Graham Land, except that no seals in a dying condition were seen.

In Graham Land the pupping season is almost exactly a month earlier than in the Ross Sea area, the first pup being found on 9 September and the height of the season being about 23 September. On 13 September a male emerged alongside a berg with blood round its mouth and fresh bleeding wounds on and under its fore-flippers. The axilla, after the genital orifice, seems to be the most favoured point of attack. In some males the genital opening, instead of being flush with the general surface of the belly, has been so maltreated that it appears as it were at the summit of a small volcano, surrounded by a series of suppurating tears and radiating gashes. Many bulls, however, seem able to pass through life without sustaining such injuries from the teeth of their fellows. Fighting, on the whole, plays little part in the life of the species.

Whether this fighting between the males is of any value to the species is doubtful. The fighting seems to be at its height at about the time of pupping, which is about 7 weeks before the time of copulation. On this account it is difficult to believe that the fighting can have much selective influence in determining which bulls shall father the succeeding year's pups.

DENTITION

The formation, function and fate of the teeth in the Weddell seal are all peculiar in one way or another. Tims (1923, p. 416) states that: "The milk dentition is very feebly developed in all seals; in the *Otaria* . . . which of all the seals most closely approaches to the terrestrial carnivora in other characters, the milk teeth are retained for a few weeks, but in most others they are shed at about the time of birth." Likewise in the *Odoboenidae*, the milk teeth are visible for a while after birth (Cobb, 1933). In many seals, however, among which are the Weddell and the Crabeater, the milk teeth are not even retained until the time of birth, but are re-absorbed at an earlier stage, the foetus at full term having the permanent dentition in a nearly functional condition.

In the Weddell seal gestation is about 10 months, the pup being born at a length of about 48 in. (125 cms.). Yet even so early as the third month, the foetus at a length of about 23 cms. already possesses the complete vestiges of the milk dentition—I 2/2, C 1/1, PC 3/3, as shown by X-ray photography (Plates I-IV).

The milk dentition seems to reach its maximum development in the fourth month of pregnancy at a length of about 33 cms. At this stage the permanent set is already making its appearance, the large lower canines, upper canines and second pair of incisors being the first to become visible. By the time the foetus reaches some 36 cms. in length the milk dentition is being reabsorbed, while the positions of three permanent post-canine teeth (i.e. premolars) are becoming obvious. At a length of about 50 cms., when the foetus is at half term, the reabsorption of the milk teeth is progressing, the incisors having become minute, while the permanent teeth are rapidly increasing in size. The permanent premolars are just visible and the molars are beginning to make their appearance. X-ray photography of the foetal material available, both of the Weddell and the Crabeater, shows the presence of three post-canine milk teeth in both upper and lower jaws. Tims (1923, p. 416) states that "the first premolar has no predecessor either in this animal (i.e. *Otaria*) or in the Phocidae. The incisors, however, vary in number in different groups, while the canines, premolars and molars are constant." These observations were made before the days of X-ray photography, when dissection was the sole means of discovery. The present series of Weddell and Crabeater foetuses, examined by the newer method, suggests that at least in these two species the above statement needs modification. The first three milk post-canines seem to be exactly in the positions that later are occupied by the first three permanent post-canines, and the latter appear to be directly successional to the former. If this be so, the adult dentition of the Weddell and Crabeater seals must be looked upon as I 2/2, C 1/1, PM 3/3, M 2/2, rather than as PM 4/4, M 1/1.

Lindsey (1937) from his extensive observations on the pups of the Weddell seal, makes the following remarks (p. 136): "Usually the four canines pierce the gums before birth, and sometimes the two outer incisors of one or both jaws. Typically the first incisors to appear were the outer ones of the upper jaw at 0-2 days of age. In only four individuals did incisors (outer) show first in the lower jaw, and in two other cases the outer incisors of both jaws came at the same time. In one pup the inner incisors were first in the upper and the outer first in the lower jaw. Never were all four upper incisors to be seen until the outer incisors of the lower jaw had been cut; and never all four lower incisors until all four upper had appeared, since the inner incisors of the upper jaw preceded those of the lower. On the average all eight incisors had appeared by 9 days, though sometimes as early as 2 or as late as 24.

"The post-canine teeth show more variation in the order of appearance. Two young displayed these teeth in the upper jaw first, and another had them simultaneously in both. In the remaining pups the first cheek teeth appeared in the lower jaw at 0-8 days, average 4.2 days. In half the cases the fifth alone was the first pair to be cut, in the rest the second pair alone, or combined with the first, third, or fifth. In the upper jaw likewise the fifth preceded all others in slightly over half of the seals, and those remaining showed the fourth alone and the fourth-fifth together as equally common, while each of four other combinations occurred first in only one pup. The first appearance of a post-canine in the upper jaw was in 0-22 days, averaging 7 days. The typical formula at the end of the first week, therefore, is:

$$\text{I. } \frac{2-2}{\text{outer pair only}}. \quad \text{C. } \frac{1-1}{1-1}. \quad \text{PC. } \frac{5\text{th pair}}{5\text{th pair}}.$$

The full set of teeth in the lower jaw comes well in advance of completion of the set in the upper. The last of all teeth to appear are, with few exceptions, the first or second pair of post-canines in the upper jaw. One individual had a complete set of teeth at 16 days. The set of another was still incomplete at 50 days, but since the missing pair was the fifth (ordinarily the first cheek teeth to appear), perhaps these were not destined to develop in this seal. The average for attaining a complete dentition is 34 days."

Thus the complete set of permanent teeth is in a fully functional condition before the end of the period of lactation, and the young animal is ready in advance to assume the adult diet.

As a result of his work on the Antarctic seals Wilson (1907, p. 46) states: "In all the seals, with but very few exceptions, the variation in the dentition is so excessive, that one is led to doubt the advisability of laying so much importance on this one feature." In a consideration of the proper affinities of the Ross seal, arguing from the extreme variation of its dentition, Wilson goes on to suggest that the Weddell shows fewer variations in its dentition than most species of seals. He states that the Leopard and Crabeater are remarkable in showing no tendency whatever to vary from the normal type with PC 5/5, while in the Weddell the only aberrant examples he found in a series of about 40 skulls were two in number, one having an extra post-canine on one side of the upper jaw, the other having it on both sides. Among about 90 Weddell skulls from Graham Land, however, the aberrant dentitions are proportionately more numerous, 6 individuals (4 females and 2 males) having

PC. $\frac{6-6}{5-5}$, while one male has PC. $\frac{6-5}{5-5}$. Skull No. 28 (a female) is especially unusual.

Whereas on the left side the supernumerary post-canine seems, as is usual, to be the most posterior in the series, that on the right is a small tooth on a level with and on the inner side of the first post-canine. The spacing of the post-canines in this animal is also unusual. In the normal skull the post-canines of the two jaws alternate, the last in the upper series being behind the last in the lower. Here, however, post-canines numbers 3, 4, and 5 in the lower jaw bear directly against the tips of 3, 4, and 5 on the right side, and numbers, 2, 3, and 4 on the left side of the upper jaw. In addition lower PC 1 on both sides actually bears against the hinder part of the upper canine. The cases of aberrant dentition in the Weddell seal are clearly more numerous than Wilson had supposed from his series of skulls.

A number of further minor points with regard to the dentition of the Weddell seal are worth noting briefly. The second pair of upper incisors are becoming caniniform though as yet their size relative to the canines is variable. Likewise one would suppose that the first pair of incisors in both jaws is becoming vestigial, their size and arrangement being very variable. Sometimes they are well spaced and of moderate size, sometimes crowded together and minute, and occasionally the inner incisors of the upper jaw do little more than lie on the surface of the palate, sockets being scarcely existent. The first upper post-canine is frequently pressed right up against the posterior side of the canine, and the sockets may be confluent. The second upper post-canine is usually the largest tooth in the post-canine series in either jaw, and often tends to be set somewhat across the line of the others. The fifth upper

post-canine is usually some distance behind the other members of the series, just as it always is in the Atlantic or Grey seal (*Halichoerus grypus*).

TOOTH WEAR AND MORTALITY

But of more practical interest than these aberrant dentitions is the fate of the teeth in the individual animal. Here there is a great contrast between the post-canines and the more anterior teeth. The post-canines normally persist throughout the life of the animal in almost perfect condition, the extent of their use in feeding clearly being insufficient to wear them down appreciably. They act simply as interlocking pegs and are of use in grasping the soft-bodied creatures (fish and Cephalopods) that are the food of the species. The fate of the anterior teeth is, however, very different, owing to their use by the animal in ice-sawing in the winter. Wilson (1907, p. 22) remarks: "The seal fixing the canines and incisors of his lower jaw in the solid ice, begins to revolve the upper jaw about them, in this way using the teeth of the lower jaw as the fixed point of a centre-bit while those of the upper act as the cutting edge." Lindsey (1937, p. 133) on the other hand describes the process as "swinging the entire head from side to side with the mouth held open at an angle of about 150°, they cut a double groove by use of the canines (and perhaps incisors also) of both jaws. In one case a seal in the water rasped away the margin of the exit hole with the upper teeth alone, without those of the lower jaw touching the ice." Whatever the precise method of ice-sawing (conditions in Graham Land were not favourable to a detailed study of the point) it is perfectly clear that this is the cause of the excessive wear of the anterior teeth in the older animals. The teeth most affected are the upper canines, then the lower canines and outer pair of upper incisors. The inner pair of upper and the outer pair of lower incisors sometimes become involved in the process, but the inner pair of lower incisors are only rarely found to have done so. Wilson (1907, pl. III) figures a typical example of the excessive wear that may occur in this way in both jaws, the anterior caniniform teeth being reduced to rounded stumps. The extent of this process will largely depend on the severity of the winter conditions. For example the necessity for keeping breathing holes open through fast-ice for 2 months will lead to less wear than if the process has to be maintained for 8 months. The ice-sawing teeth of young Weddell seals that have had to spend but a single winter beneath the ice already show some wear of the tips.

Colyer (1936) in a consideration of tooth 'abrasion' questions a statement of Underwood (1914) in connection with the precise method of wear of Weddell teeth. Colyer agrees that the observed wear of the canines and caniniform teeth of this species is due to ice-sawing, but points out that the phenomenon is different, both in origin and appearance, from the condition of 'abrasion' of the teeth of Otariids and a few other mammals.

Though there can be no doubt of the cause of the wear of the teeth in the Weddell seal, an almost precisely similar appearance of the canines has been observed, among others, in a skull of a Jamaican seal (*Monachus tropicalis*) from the West Indies, where such an origin is clearly quite impossible.

The wear of the tips of the teeth is not of itself of importance, until the stage is reached at which the tooth cavity becomes exposed, either simply through wear or

through actual fracture. Once the cavity is exposed consequences follow rapidly; abscesses are formed, necrosis sets in, at first simply round the tooth with the exposed cavity, but soon extending over a far wider area. In time the necrosis may become so serious that the first affected teeth loosen and drop out, to be followed later by others, while drainage channels appear on the palatal and external surfaces of the maxillae, (plate VII). In one case, that of a female probably 5 or 6 years old, the necrosis consequent upon the breakage of the left lower canine has been so excessive that the lower jaw has separated into two parts. The part on the left bears the post-canines of the left side, that on the right bears in addition to its normal complement both incisors of the left side.

The ice-sawing teeth of the Weddell seal are certainly of great importance for successful life below the fast-ice. It seems highly probable that extensive damage to these teeth, as described above, will seriously affect the ability of the individual to maintain itself in such circumstances. Indeed, it seems highly probable that here we have a very potent factor in the mortality of the species. Once the ice-sawing teeth are so worn or fractured that the tooth cavity is exposed, necrosis sets in, and soon the seal will become incapable of keeping open the necessary breathing holes. The individual then must die by drowning unless it can maintain a precarious existence, dependent upon the labours of its fellows. This factor of tooth wear and breakage very probably is the major cause of mortality in the species, once the adult stage has been reached. It is a factor that probably is unique among mammals, and one which apparently comes into operation after a rather small number of years. As shown in a later section of this paper, probably very few female Weddell seals live to pup more than five or six times. It would be of great interest to study from this point of view the small colony of Weddell seals at South Georgia, where the animals are free from the necessity of ice-sawing in winter. There the animals might live to considerably greater ages than in higher latitudes.

It would seem in fact from this consideration of tooth wear that the Weddell seal is living in a habitat to which it is not as yet fully adapted. Most Pinnipeds have the outermost pair of upper incisors sub-caniniform, but in the Weddell the process has gone farther than in other species, the beginning of adaptation to the necessity for ice-sawing. Considerable changes in the dentition, however, would be required before the life of the individual could be much prolonged, unless the use of communal breathing holes became the normal circumstance. Food supply within the radius of the normal dive would probably eventually set a limit to such a habit, but the food being free-swimming fishes and Cephalopods, one imagines that the limit would not be reached for some time.

There are virtually no animals that prey on the Weddell seal. The Killer whales which, to judge from the scars upon the bodies of the survivors, play such havoc with the Crabeater seals, scarcely haunt the coastal waters closely enough to come in contact with the Weddell seal, a point remarked upon both by Wilson (1907) and by Lindsey (1937). Weddells do sometimes drift far from the coast asleep on floes and may then fall victim to the Killer whales, but probably this does not often happen. Certainly Weddell seals are never found with great scars upon their bodies as are the Crabeaters, but this may have one of three explanations, either that they never meet the Killer whales, or that they never survive when they do meet, or that,

on meeting, the seal is sufficiently skilful in the water to escape unmarked. Leopard seals probably sometimes take the pups of the Weddell, or the young ones when still fairly small. The extent of this possible loss is entirely problematical, the Leopard seals normally feeding on penguins. Leopard seals have, however, in the Falkland Islands been seen to fight with the Sea Lions (*Otaria byronia*), and seal remains have been found in Leopard seals in the Antarctic proper. Losses among the Weddells from this cause are likely to be very small, if more than occasional.

The gut parasites that regularly infest the Weddell seal in prodigious numbers may possibly be a potent cause of mortality. These will be discussed at length in a later paper.

Fighting among the males is certainly one cause of mortality, but whether it is really frequent, or has simply had undue attention owing to the striking circumstances, it is not possible to say. Lindsey (1937) has already been quoted with respect to the finding of several bulls that were believed to be bleeding to death from fights with others of their species, and scarcely able to move. More vivid is Wilson's description (1907, p. 20) which applies to both the Weddell and the Crabeater seal. "At the close of the rutting season which follows directly upon the separation of the young ones from their mothers, it is noticeable how often one may find the bulls in secluded places, to which they have retired with a multitude of open wounds. This bears upon the discovery of dead seals, not only in secluded spots, but in places which one would have thought almost inaccessible to them." Thus the discovery was made "of dead seals at a distance of 35 miles inland from the coast, and on the surface of a glacier no less than 3000 ft. above sea level. In these cases the carcasses were those of Crabeaters; again the carcasses of Crabeaters were found . . . in the Royal Society's Range 2000 ft. above sea level, and 30 miles inland. Yet another was found on New Harbour Glacier, 200 ft. above sea level and 20 miles from the coast. The carcass of a Weddell's seal was found . . . 2400 ft. above sea level, on a similar glacier, and other seal remains at similar heights and distances from the coast . . . and, still further in (i.e. more than 20 miles), an old and battle-scarred male, alive (Weddell) and covered with suppurating sores, more than 20 miles from any of his kind."

Lindsey (1937, p. 139) cites several other causes of death in the Weddell seal population that came to his notice, most of which can be classed as 'accidental'. "Two pairs of twins did not survive birth. Another frozen and flattened pup was found with its viscera protruding through the ruptured abdominal wall, probably from the mother rolling upon it . . . Another young one had died when almost out of a water-hole, having been caught by its weight in a small V-shaped gap between ice blocks. The extreme flexibility characteristic of a seal's thoracic wall had caused it to be suffocated. In one case a pup had swum to an isolated hole in the pressure ice and never was located by the parent. The hole froze over and starvation was inevitable. . . . Siple estimated the pup mortality at 10 per cent. . . . The 1934 mortality in one rookery [was] at least 18 per cent." Several deaths were among pups "less than 20 days old, and probably they were drowned beneath the ice through inability to find a blow hole." Such are some of the causes of death recorded by Lindsey among the young Weddell seals in the Bay of Whales.

A number of other maladies to which the Weddell seal is prone were noticed in Graham Land. Though by no means all likely to cause death in the cases seen, these

are at least indicative of further causes of mortality. The wounds of seals always seem to heal very slowly, after much suppuration, and this is certainly very true of the Weddell. The bites received in fights fester badly before healing, as do the gashes that are sometimes seen, due probably to sharp points of rock or ice. Pus-filled cavities were not rarely found in the axilla, on the rump and between the hind limbs and tail. Sometimes there was an obvious drainage to the exterior, sometimes not. In the former case occasionally the seal would leave behind it on the ice a trail produced by a continuous dribble of pus and blood. These pus-pockets were often bigger than a fist and the appearance of the surrounding tissues suggested that they were of long standing. One or two seals so afflicted were found to be in extremely poor condition, the blubber layer being thin and fibrous instead of thick and oily in texture. Presumably due to continued suppuration were a few cases, notably an old male taken on 4/10/36 in a rift in the shelf-ice of King George VI Sound, in which the flesh had rotted back from the extremities of one or more toes to leave a few inches of rotten bone projecting.

One adult female (20/9/35) that had just pupped was found to contain a large kidney stone, about $1\frac{1}{2}$ in. in diameter, in the left ureter. Another adult female taken on 29/2/36 had a number of hard fibroids in the uterus, the largest of which were 2 in. and 1 in. respectively in diameter. She was not pregnant and the state of her ovaries (No. 1454) is discussed in a later section.

There must also be mortality from accidental crushing, particularly when emerging through unstable ice in tide cracks. In Labrador indeed it is quite common for men to go out in the spring with the definite purpose of hunting for seals so crushed in the course of the preceding winter. Doubtless the same thing happens with the Weddell seal. Even if not killed outright, the seal may be badly damaged. A female taken at Deception Island in January 1935 had a broken scapula, the two halves of which had formed an almost perfect pseudo-arthritis. Another female that had evidently been badly crushed, but had just escaped, was killed on 20/12/36. The rear half of the body was completely paralysed and was simply dragged over the ice in a slightly twisted position. From the locality in which the seal was found, however, it must still have been capable of swimming. There were a number of open suppurating wounds in the hind part, particularly around the genital orifice, and there was continuous drainage to the exterior. The thin black pigmented outer layer of the skin was stripping off in sheets, but the rusty coloured premoult hair was still firmly fixed. When the body was opened there was a strong smell of putrescence and the whole animal was very emaciated, the blubber being scarcely 1 in. thick. The seal was quite unfit as food for men or dogs.

It is clear that the Weddell seal is open to a number of maladies, but the relative importance of these in making up the total mortality is unknown. One might surmise that the chief mortality is among the pups, that then for a number of years the adults suffer rather few losses, and that finally most deaths occur under the winter ice by reason of the seals failing to keep open the necessary breathing holes. In this last process, as already suggested, any breakage or rotting of the teeth may be a severe handicap and lead directly to the failure of the animal to maintain itself.

REPRODUCTION

COPULATION

Copulation has apparently never been seen in the Weddell seal. It is therefore certain that it occurs in the water, since otherwise it could scarcely have failed to be observed. Knowledge on the subject is scanty, but it seems that aquatic copulation is usual among the Phocids. Iversen (1927) never saw the copulation of the Harp seal, and assumed that it took place in the water, and Havinga (1933) holds the same opinion of the Common seal. The Elephant seal regularly copulates on land (Matthews, 1929, *et al.*), and the Grey seal apparently sometimes does so on land and sometimes in the water (Fraser Darling, private communication). In contrast, the less aquatically adapted Eared seals regularly copulate on land, so far as is known. Both Allen (1880), and Elliott (1881), however, mention that sometimes the Northern Fur seal of Alaska (*Callorhinus alascanus*) will copulate in the water. No certain knowledge seems to be available on this subject for the Pacific and Atlantic walruses (*Odobaeus obesus* and *O. rosmarus*).

The close connection between the maintenance of the harem system and terrestrial and aquatic copulation is considered in a later section of this paper.

THE PRODUCTION OF SPERM

The amount of testicular material, from the Weddell seal, collected and brought home for examination was much less than wisdom should have dictated. Because of this lack of material it is not possible to state at what age the male seals start to ripen sperm, nor precisely for what period each year they are in possession of it. Chapsky (1936), speaking of the Walrus, states that the condition of the testes (the number examined seems to have been small, but is not stated) "indubitably testifies to a cyclic activity of the sexual glands." Testes from six adult Weddells only are available. These have been sectioned, and below are set out the results so obtained.

1228	10/11/35	97 in.	Plenty of sperm.
1500	30/11/36	90 in.	Moderate numbers of sperm.
1374	11/1/36	87 in.	No sperm.
1392	17/1/36	93 in.	<i>ditto</i>
1394	17/1/36	97 in.	<i>ditto</i>
1468	8/3/36	85 in.	<i>ditto</i>

It is seen that in November ripe sperm are present in abundance, but that thereafter they soon disappear. How long previously there had been abundance of sperm is unknown. It would be imagined that the fighting between males, which apparently starts at about the beginning of the pupping season, would be unlikely to take place unless the males were already then in full breeding condition. The small amount of evidence suggests that the males ripen their sperm in plenty of time, begin to fight among themselves at the time when the females are pupping, and are

ready to serve the females as soon as the latter are willing to receive them. The evidence from the females as to the length of gestation (10 months less a few days), suggests that copulation takes place at about the time of the permanent separation from the pups (i.e. about 7 weeks after pupping). Thus in Graham Land copulation probably usually takes place about the middle of November. From the evidence of the testes it is seen that the sperm is ripe at this time, but that soon afterwards the males are probably going out of breeding condition. If the males normally go out of condition at an early date and the females are not ready to copulate until a certain time after pupping, here is clearly a mechanism that may be important in controlling the regularity of the pupping season from year to year.

This tentative conclusion may be compared with Hamilton's finding for the Southern Sea Lion. He states (1939, p. 143): "There is no clearly marked anoestrous period, but immediately after the breeding season there may be a time of more or less complete azoospermy, depending on the recent history of the individual."

GESTATION AND THE GROWTH OF THE FOETUS

Wilson (1907, p. 19) remarks: "The gestation period in the female is as nearly as possible 11 months." Unfortunately he does not set down the evidence for the remark; no mention is made of copulation having been observed, but he had just spoken of "the severe fights [i.e. among the males] which take place in the third week of October, and in November and December." The pupping of the Weddell seal in the Ross Sea is at its height in the third week of October. Wilson's estimate of the period of gestation is therefore probably based on the observed fighting season of the males. Rudmose Brown (1915) estimated the period of gestation as probably 8 to 9 months from the size of foetuses taken in the first half of the year.

Lindsey (1937, p. 130) bases his estimate of the period of gestation on the following argument. "Forty-four births of known date were recorded, from 5 October to 10 November, in the rookery studied, including both 1929 and 1934 seasons. The median date is 23 October; also the median birth occurred on this date. Since small embryos were found as early as the latter part of January, the gestation period seems to last over 9 months. The rarity of bulls in the central and southern parts of the bay [where the rookeries occur] while the mothers and pups are together, may aid in setting its maximum. Eighteen of the dated young were traced through the time of permanent separation which occurred on the average 50.3 days after birth, or about 12 December on an average. Bulls become common in the rookery area after the first week of December. The gestation period probably does not exceed 10 months and 10 days, although it may be somewhat less." Lindsey's argument from the absence of bulls in the rookery is not necessarily valid. It has already been shown that fighting can and does, and copulation must, take place in the water, since it has not been observed on land. Lindsey's statement as to the absence of bulls must be based on sexing the animals on land; if the bulls remained in the water at this period it would appear to him that they were absent. He continues (p. 140): "Fights are not strictly confined to the mating season, for freshly wounded bulls were seen as early as 15 October. The few males appearing in the rookery during this month and in November were either wounded or were very old individuals." These last were

probably the most damaged in the aquatic sexual battles, which surely suggests that the more successful males were present in the area at the same time. Thus, though Lindsey may be quite correct in stating that the gestation "does not exceed 10 months and 10 days, although it may be somewhat less", the observations he quotes are not incompatible with Wilson's belief that it lasts "as nearly as possible 11 months".

In Graham Land, where pupping takes place just one month earlier than in the Ross Sea area (i.e. is at its height in the third week of September), a variety of circumstances made observations on the Weddell population, in the weeks soon after the birth of the pups, very difficult. Chief among these was the early break-up of the sea-ice immediately around the small islands on which was situated the Expedition's base in 1935, and in 1936 the absence of the author on an extended sledge journey.

Certain points are clear, however. The males tend to lie out on the ice in proportionately much greater numbers than the females during August, the ratio being about 3 males to 1 female. During the pupping season (i.e. roughly a month starting with the second week of September, or perhaps a little later in southern Graham Land) the number of males seen out on the ice is very small. The few seen at this time had fresh wounds, more or less extensive, but none were in the serious condition mentioned by Lindsey. In the latter part of October and in November the numbers of the two sexes seen lying out were more nearly equal, as was the case in succeeding months. The scarcity of males seen on the ice during the pupping season can perhaps partly be accounted for by the interest taken by the observer in the young seals, so that he failed to go aside to examine the sex of seals lying by themselves at a little distance. It is clear that the males are present in the area before, during, and after the pupping season, though there may be variations in the frequency with which they leave the water. Nothing more definite is, in fact, to be learned from the observed behaviour of the seals as to their precise mating time.

A consideration of the embryonic material may lead to a more certain conclusion on this point. Lindsey (1937) remarks that small embryos were found in the latter part of January, the height of the pupping season in his area being 23 October. In Graham Land, with the pupping roughly a month earlier, the first embryos were taken on 6 January. At this date one was already 3.5 cms. in length, another 1.5 cms. In other cases at this date swellings the size of a pigeon's egg were seen in the uterus, clearly indicating the presence of a small embryo, but in most instances rough and rapid butchery in the field prevented the extraction of these tiny embryos which were 0.5 to 1 cm. in length. A fortnight later in a more northerly area, where the seals might be expected to be in advance of those some hundreds of miles to the south, a foetus of 15.4 cms. was taken on 22 January. The lengths of a number of embryos and foetuses are set out graphically (fig. 1). to show the approximate rate of growth. It is probable, but not certain, that very early in life the embryos always develop at the same rate. The rate of growth of the embryo in the early stages certainly varies from species to species. In man, apparently, it takes more than a month for the fertilized ovum to become an embryo 1 cm. in length. If the same rate of development be assumed for the Weddell seal, copulation would take place near the beginning of December in most instances, a week or two earlier in a few. This would make the probable period of gestation a little less than 10 months. Until more is known of the

rate of growth of the Weddell embryo in the early stages, that is the most accurate estimate that can be made from the present material.

A study of the ovaries preserved from the Graham Land seals can give a further helpful indication of the time of copulation. It seems almost certain that the corpus

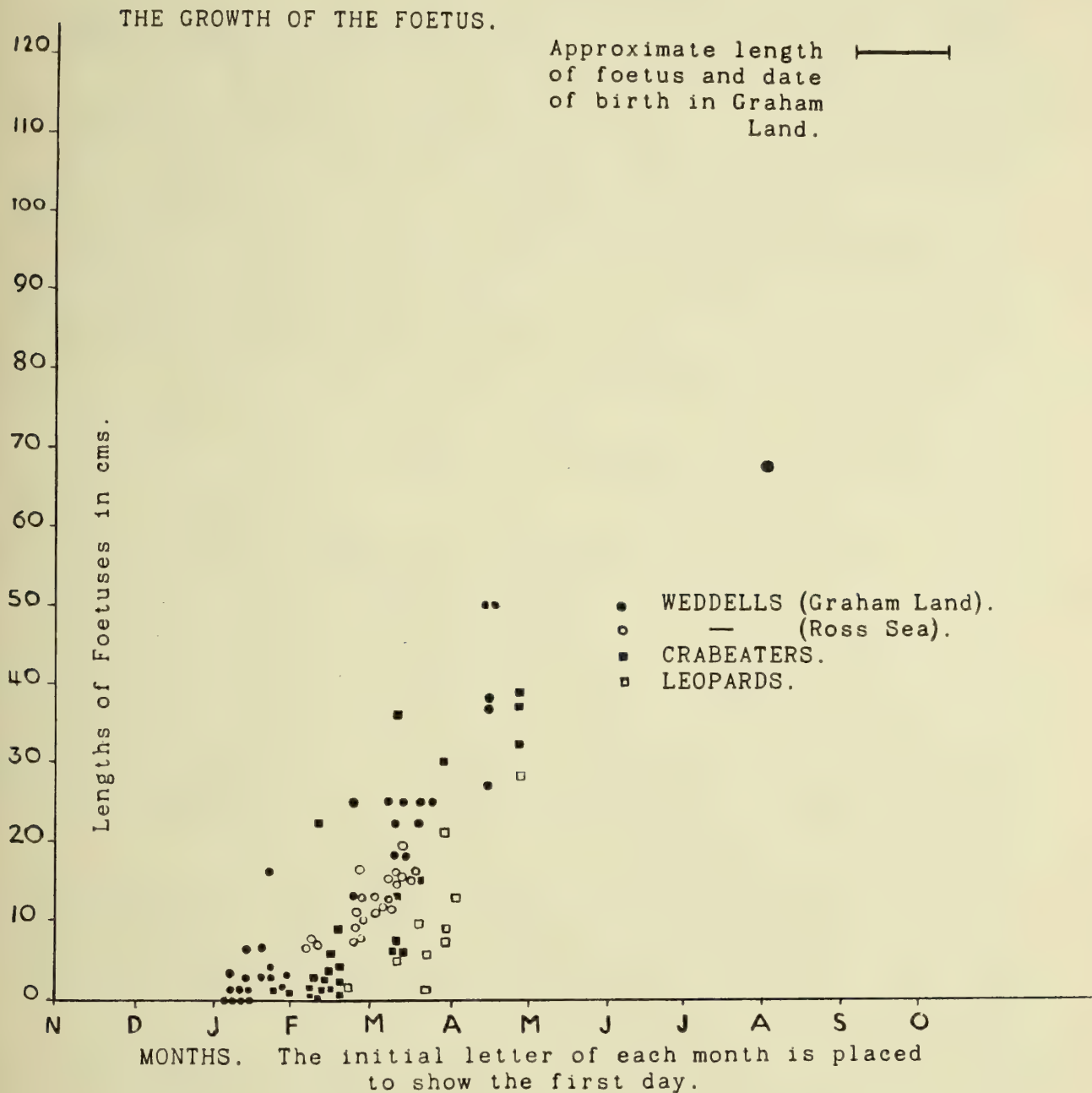


FIG. 1.—Lengths of foetuses are shown in relation to the dates at which they were taken. The smallest embryos were about 1 cm. long, and it is probable that they were then about 1 month old. The pupping time in Graham Land and the average length of the pup at birth are shown by a line. The Weddells in the Ross Sea pup about 1 month later than in Graham Land, and figures provided by Marett Tims (1910) are inserted for comparison. The figures for the Crabeater and Leopard seals are all from Graham Land.

luteum of pregnancy develops with sufficient rapidity for it to be of large size before pregnancy is obvious from cursory examination of the uterus. By the time that the embryo is 0.5 to 1 cm. long its foetal membranes have formed in one or other of the two uterine horns, a swelling the size of a pigeon's egg which is obvious from the outside. The number of female Weddells available for investigation in November and December was not great, so that the ovarian material is not as extensive for this period as could be wished. The first ovaries to show a corpus luteum of the new season were taken in the last few days of November and thenceforth they became common. The small embryos were becoming visible at the beginning of January. In other mammals the corpus luteum usually develops very rapidly after ovulation (e.g. Hammond (1927) shows that in the cow the corpus is of full-size in 8 days). It becomes clear then that the earliest ovulations (and presumably copulations) are in the second half of November, more usually in the early part of December, this fact being attested both by the embryos and the corpora lutea. Sexual battles among the males apparently start at about the time of the birth of the pups, and then copulation follows shortly after the permanent separation of the cows and pups, which Lindsey has shown to take place on an average at 50 days of age. The small amount of testicular material available points to the same conclusion as to the time of copulation.

The period of gestation of the Weddell seal is thus concluded to be a few days under 10 months, unless it be found that the growth of the embryo is abnormally slow in the early part of gestation.

In the Hooded seal copulation takes place in the water at once after or during lactation. Yet the embryo apparently is not easily visible until 3 months later, though a new corpus luteum, but of small size, is present throughout this period (Høst, private communication). Likewise Nansen (1925, p. 62), in speaking of the Harp seal, states: "It appears probable that there must be a kind of pause in the development of the embryo during the first period," basing his view on the fact that he found embryos only $2\frac{1}{2}$ in. long 4 months after the known period of copulation. Likewise Chapsky and Kovolev (1938) state that gestation in the Bearded seal is 11 months, while development occupies 9 to $9\frac{1}{2}$ months. Very slow development of the embryo in the early stages is also well known in the Roe deer (Millais, 1906; Zuckerman, 1932) where gestation is 40 weeks, but the embryo remains minute during the first half of this period.

In the graph (fig. 1) the lengths of the Weddell foetuses (also of Crabeater and Leopard foetuses for comparison) have been set out against the dates at which they were taken. In this way are obtained both a clear picture of the type of growth curve that the foetus follows, and some idea of the amount of variation that can occur even when the pupping season is limited to 4 or 5 weeks. Estimation of the approximate date of conception of the majority must obviously depend on that unknown factor, the time taken for the fertilized egg to develop into an embryo about 1 cm. long. In the discussion above, this period has been assumed to be about a month.

Included in the graph of foetal lengths are some data derived from Tims' (1910) paper on Weddell foetuses collected by the *Discovery* Expedition. From these it is clear that the Ross Sea foetuses are from 3 weeks to a month behind those in

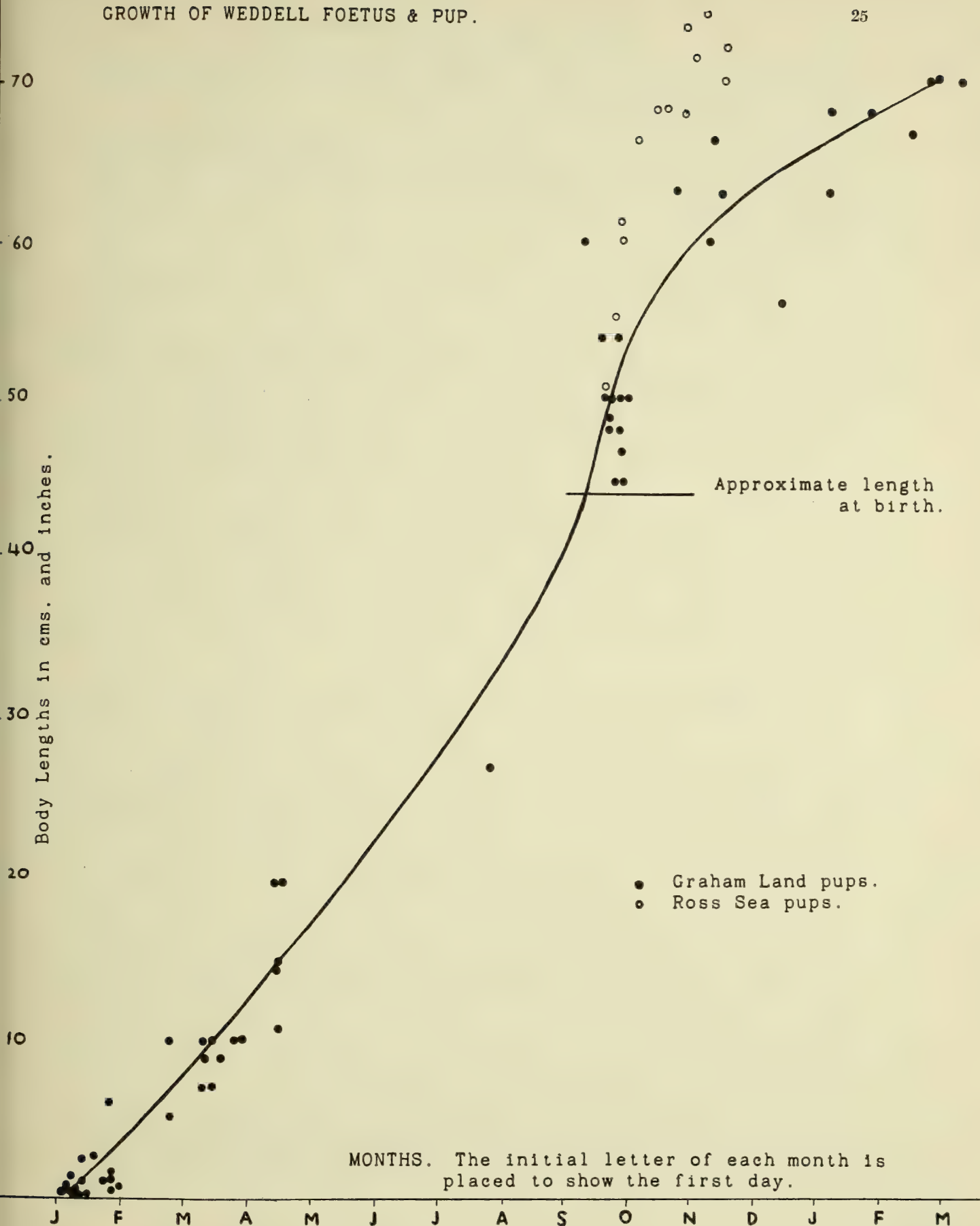


FIG. 2.—The growth of the Weddell seal in Graham Land is shown from conception to a length of about 6 ft. The growth of the Weddell pups (with known age in days) measured by Lindsey in the Ross Sea are inserted with 15 September as a standard date of birth. The greater size of the Ross Sea pups is probably due to differences in the method of measurement (i.e., amount of stretching), though it is possible that they represent a real greater initial length and/or rate of growth in the first few weeks.

Graham Land in date, which fact tallies with Lindsey's (1937) finding that the mean date of birth of the Weddell pups in the Bay of Whales was 23 October, while in Graham Land it was about a month earlier.

The growth of the foetuses in another diagram (fig. 2) has been linked with that of the young seals up to a length of 70 in. The curve so obtained clearly demonstrates the accelerated rate of growth during the short period of lactation, a subject that is enlarged upon in a later section of this paper.

PARTURITION

For some hours or days before pupping the expectant females lie out at the chosen place, usually the sea-ice in some protected bay or channel. If disturbed at this time they usually move off to some other place. When lying out shortly before pupping, the females have a rather typical attitude, lying stretched straight out and half over on their backs. Low moaning noises are sometimes made and uterine contractions may be visible externally. The actual birth of the pup does not seem to have been observed in this species, though various workers have examined the pups very shortly before and after birth. It is evident that parturition is a rapid process. In one instance the chief engineer of R.Y. *Penola* observed two females lying together, the one with a pup, the other without, but obviously expectant. He went on a few yards to shoot a Sheathbill, and at the sound of the shot one of the Weddells set up a mooing noise like that of a cow. When he returned about 5 minutes later the second female had a pup and there were pools of blood on the ice. The umbilicus had been severed but no placenta was visible.

Wilson (1907, p. 18) remarks: "Their eyes are open at birth, and the involution of the umbilical cord takes several days. The young seal is found at times with the cord intact, attached to the expelled placenta. Presumably the cord is bitten through by the mother, though we did not see this done." Lindsey (1937, p. 135) on the other hand says: "The umbilical cord is not bitten through by the female, but evidently has a weak spot where it is broken by the young or by the mother in moving about. The break occurs 3 or 4 in. from the umbilicus, and the pup carries the conspicuous stump for from 5 to 11 days before it drops off." Rudmose Brown (1913, p. 190) states: "It was noticed that the umbilical cord is severed by the young seal breaking it at birth; it is not bitten through by the mother." The teeth of the Weddell seal could scarcely be efficient implements for severing a fleshy cord. Matthews (1929) p. 236) with regard to the Elephant seal, remarks: "The umbilical cord, which is black and 2 ft. long, is sloughed off about 3 days after birth. The piece attached to the new-born pup is from 12 in. to 18 in. long. It was not ascertained if the cord is bitten asunder by the mother at birth, or if it is merely broken, but it is fair to assume that it is broken, first because of the ragged appearance presented by the free end, and secondly because the teeth of the mothers are capable of being used for seizing objects but not for cutting them." The rubbish of membranes, placentae, etc., are in all cases soon devoured by the attendant gulls. One would hesitate to suggest that the gulls have fore-knowledge of this food supply, but certainly their behaviour, perched on the ice near the parturient seals, gives the impression of expectancy.

NUMBER OF PUPS AT BIRTH

The normal number of pups at a birth in all seals is one, and this is certainly the case in the Weddell sea. Tims (1910, p. 19) states: "Mayer, quoted by Turner, records an instance in *Phoca vitulina* in which the left horn of the uterus contained five embryos and the right horn four. Turner also has in his possession twin foetuses from the uterus of *Phoca groenlandica*. There can, however, be no doubt that the presence of more than one foetus is quite exceptional, and that the foetus is situated in one or other of the cornua, the non-gravid horn being very slightly, if at all enlarged." Wilson (1907, p. 19), remarks with reference to the Weddell seal: "In the absence of the mother the young one would occasionally make its way to a neighbouring seal, and, if she happened to have a young one too, one might be misled into thinking that she had given birth to the two herself. Quite probably this happens sometimes, but we were never quite sure of such a case." Lindsey (1937, p. 135) has more precise knowledge on the subject to offer: "Except in rare cases a female produces only one pup a season. One pair of fraternal twins was seen in 1929, and another in 1934, but all four were dead when found and probably had been born so. These pups weighed about 50 lb. each. A female collected in the fall contained two small embryos, both in the same horn of the uterus."

In Graham Land among more than 100 pregnant and parturient females examined, there was only found a single case of twinning. In mid-April a female of 86 in. was killed which contained in the same horn of the uterus two foetuses, each 50 cms. in length, the one male, the other female. These foetuses were well up to the average size for the time of year, which represents about half-way through pregnancy. These twins were completely separate as to their foetal membranes, and were therefore binovular twins, a fact that was confirmed by the presence of two corpora lutea side by side in the ovary of the same side as the horn of the uterus in which they lay.

Twinning in the Weddell seal is evidently rare, but does sometimes occur. Whether it is ever completely successful is doubtful; the strain upon the mother in providing milk for a single pup to increase in weight by 7 lb. daily is clearly great, to judge from the decrease in her total weight, and one doubts her ability to provide in this way for two pups simultaneously.

Sclater (1900) speaking of the Cape Fur seal (*Arctocephalus antarcticus*), the only South African Otariid, states quite definitely however, that in that species there are normally two pups at birth, that gestation is 12 months, lactation 6 months, and that stray pups are commonly accepted by other females. No confirmation of his statement appears in the literature, and Sclater provides no clue as to the source of his affirmation. There is little doubt that the statement is quite incorrect.

THE SEX RATIO

In seals, both polygynous and non-polygynous, it is generally believed that the sex ratio is approximately equality. In the Weddell seal a study of the sex ratio of the adults is not really satisfactory. The seals can only be sexed when lying out on the ice or on beaches, and therefore there is an underlying assumption that the

behaviour of the two sexes is the same, if the figures obtained in this way are accepted. A sex ratio based on the adults seen or killed out of water can then only be accepted with reserve as an indication of the sex ratio of the population as a whole. Below are the figures month by month of the Weddell seals killed in the course of the British Graham Land Expedition 1934-37, including those seals that were not sexed, and new-born pups.

WEDDELL SEALS KILLED IN GRAHAM LAND
1934-37

Sex.	1934	1935												1936	
	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Males ..	—	4	0	1	29	0	2	2	3	11	4	2	2	9	1
Females	—	5	0	2	40	0	1	0	0	21	3	0	2	23	1
? sex ..	64	1	0	3	22	0	0	0	0	8	0	0	0	0	0

			1936										1937					
													SHORE			SHIP		
Sex.			Mar.	Apr.	May	Jun.	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Jan.	Feb.	Totals.
Males	7	2	0	0	7	3	2	7	4	3	4	1	0	2	0	112
Females	15	1	0	1	1	1	5	4	6	9	8	3	0	1	0	153
? sex	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0	102
																		367

There were killed in Graham Land 367 Weddell seals, 112 of these being males, 153 being females, and the remainder (102) unsexed. Except during September 1935 and January 1936 the two sexes were killed quite impartially and no selection was operating. In the two months mentioned however, this was not strictly so. In September 1935 the interest centred mainly on the new-born pups, so that there was a tendency to kill those adults that were accompanied by pups rather than lone adults. This was also one of the very few periods in the course of the Expedition when it was not necessary to kill every Weddell seal found, and undoubtedly as a result the females suffered most. Again in January 1936, when *R.Y. Penola* made a voyage to Deception Island, an undue proportion of females was taken. After a period when seals had been very scarce around the Argentine Islands, considerable numbers were found at Deception and others of the islands off northern Graham Land. At this time it was not necessary to kill many seals for meat, and a definite selection was made of the females in order to obtain their ovaries at this season and a series of early embryos. At all other times it is believed that there was no selection in the killing and that the numbers of the two sexes killed were in proportion to their frequency of lying out. If these two months (September 1935 and January 1936)

are subtracted from the totals given above, the figures remaining are 92 males and 109 females, which is equivalent to 84.4 males to every 100 females.

As explained above this ratio may or may not be correct, according to whether it can fairly be assumed that the frequency of lying out of the males and females is the same. The figures of killings month by month are too small to be really helpful in defining differences in habits between the sexes. The figures for April 1935 are the largest in any one month, namely 29 males and 40 females. Immediately prior to the pupping season it was clear, as would be expected, that more females were lying out, having already chose the place at which to pup. For three months previous to this, in both 1935 and 1936, very few seals were seen, but it was noticed that almost all were males and the figures for killing bear this out. (A number of seals at this season were sexed but not killed as being too distant from the Expedition's base.) The figures of those killed in June, July, and August for 1935 and 1936 added together are:

	<i>June</i>	<i>July</i>	<i>August</i>	<i>Total</i>
Males	2	9	6	17
Females	2	1	1	4

In May no seals were killed in either year owing to the state of the ice, which made it impossible to come at those few that were seen lying out at a distance.

It is thus clear that the lying out habits of the two sexes of the Weddell seal do vary relatively to one another from time to time. Therefore the sex ratio calculated above of 84.4 males to every 100 females is probably not correct.

Attention may now be turned to the foetuses and new-born pups, which should form a much fairer guide at least to the initial sex ratio. The evidence from the foetuses is not as great as it should have been, as unfortunately they were not systematically sexed in the early stages of the work when they were most abundant. This is regrettable, and the foetal sex ratio is consequently based on those few that were preserved more than $6\frac{1}{2}$ cms. in length. The sex of foetuses less than some 6–7 cms. long is not readily determinable by simple examination. Of those preserved greater than this length 3 were males and 2 females.

The evidence to be obtained as to the sex ratio from the pups at full-term and at birth is a little better. The figures are as follows:

September 1935	10 males	7 females.
September 1936	14 males	0 females.

Of the pups taken in 1936 one only was sexed by the present writer, the remainder being taken in his absence. The two members of the Expedition who collected the other 13 male pups stated that they took great care to make a correct sex determination in each case, and that they were quite certain that there had been no mistake. The genital orifice in the new-born male pup, however, is small, and though the blubber is thin, the *os penis* may not be particularly obvious on skinning. Though hesitating to doubt the sex determination made in these 13 cases, it is probably safest for the present to set them on one side, simply remembering that here is a piece of

suggestive evidence that may be of importance in confirming later findings. This is unfortunate, since it reduces the number of sexed pups so heavily. The remaining pups were 11 males and 7 females, which is scarcely a large enough number from which to draw far-reaching conclusions. The suggestion is that as with man and a number of other mammals (Parkes, 1926) the males are born in rather greater number than the females. Whether in later life the proportion of males actually sinks cannot at present be determined.

A small further amount of evidence is to be obtained from the paper by Tims (1910) in which he described the Weddell foetal material brought back by the *Discovery* Expedition of 1901-04. In this collection were 29 foetuses, the smallest of which was 12 mm. in length, the largest 795 mm., and weighing 12 lb., but unfortunately nowhere in the paper is there mention of the sex of these foetuses. The only reference to this important point is on p. 18, where it is stated: "I was unable to distinguish the sexes in their earlier stages by the external characters, and it so happened that the four specimens I dissected all turned out to be males. Whether this was simply bad fortune or whether it indicates that the number of males born preponderates over females I am unable to say."

Lindsey (1937), in his study of weight increases of the pups, presumably took an unselected sample, yet of the 18 pups studied by him 12 were males and only 6 females.

A further point is the set of length measurements of Weddell pups given by Bruce (1915). There the measurements of 8 pups are shown and of these 6 were males. There is thus a possibility that in the Weddell seal the males may be distinctly more abundant than the females at birth. Brian Roberts (private communication) has provided some figures for the sex ratio of the pups at birth in the Elephant seal. His are the only figures for a species of Phocid that are in any way satisfactory. Owing to the difficulty of getting in among the cows, the pups cannot be examined until they are about a month old and have congregated at the back of the rookery. On 28/10/36 in St. Andrew's Bay, South Georgia, Roberts made sex counts of all the pups on three separate small beaches.

Beach "A"	105 males	77 females
Beach "B"	63 males	44 females
Beach "C"	61 males	40 females

Thus in the Elephant seal there is strong evidence that male pups are produced in greater numbers than female pups. The same may well be true of other species of Phocids, and, there seems to be some evidence for it in the Weddell seal.

Among the adult Weddells however, as already shown, there is not enough evidence to provide a true guide to the sex ratio. Whether the mortality among the members of one sex is greater than that among those of the other is scarcely known. If Lindsey's statement (1937, p. 140) that "several bulls were evidently bleeding to death from fights with other seals" be accepted, it is clear that here is a serious factor that affects the males alone. Whether this loss among the males is significant, or whether it is greater than essentially female losses owing to the trials of repeated pregnancies is quite unknown. Certainly there is nothing to suggest that mortality from other causes in one sex is likely to be much greater than in the other, so as to modify the sex ratio in the course of life.

LACTATION

The nipples are two in number and in the abdominal region. Normally they lie flush with the surface, and indeed the whole mammary apparatus, though each functional gland may be $18 \times 9 \times 4$ in., is invisible from the exterior owing to the thickness of the blubber. The nipples stand erect about $1\frac{1}{2}$ in. above the surface when the pup is sucking, and sometimes too, by reason of the internal pressure, when the lactating seal rolls over upon her side or back. When lactation is over the mammary glands rapidly diminish in size to the quiescent condition found throughout the remainder of the year. At birth the mammae of the pups, both male and female, sometimes contain a small amount of 'witches' milk, but in 2 or 3 days this infantile functioning of the glands ceases.

The adult female, shortly before giving birth to her pup, is sometimes seen to have a trickle of milk running down across her belly. No analysis seems to have been made of the milk of the Weddell seal. It is white and creamy, but has a somewhat unpleasant taste. The experiment was tried of ligaturing the two ends of a pup's milk-filled stomach so that it could be brought back to supply an antarctic form of the Scandinavian *skiaer* or sour milk. The clotted seal's milk was, however, too tainted with bile to form a pleasant dish for human consumption.

It is evident that the female Weddell desires her pup to suck, for she may sometimes be seen to push it with her nose close to the teats after she has taken up a position on her side. If her pup has died the female may be seen to bite it repeatedly with her teeth and drag it into position alongside her body. Even the living pup may sometimes have difficulty in finding its way to the teats. In one instance a pup was seen to start the search near the mother's tail, then with considerable efforts to wriggle all the way along her back, stopping at intervals to make exploratory sucks. It then proceeded round her head, spent some time at her neck where doubtless the folds of skin gave a promising indication, and then worked down her ventral side until at last successful in its quest.

Lindsey (1937), with his very fine opportunities, made a detailed study of the growth of the young seals, and the period of lactation and nursing. In Graham Land the young seals could not be observed in an undisturbed condition owing to the depredations of the large numbers of sledge dogs. To quote from Lindsey (p. 137): "After the birth of its young the female does not enter the water for a week or more; hence she obtains no food. The production of milk in sufficient quantity for the young to gain weight at the rate of 7 lb. daily demands utilization of much of the blubber stored beneath the skin. Even after the female starts feeding once more the blubber supply still is drawn upon, for the nursing female becomes visibly thinner each week."

"The mean age of 13 young when last observed suckling was 45.2 days. Five of these were seen nursing at from 50 to 55 days of age. The age of permanent separation of 18 young from their mothers averaged 50.3 days, which probably is also more nearly the correct average age for weaning. A marked loss of weight by the young occurs about this time. The change from a milk diet is gradual, combining amphipod and isopod crustaceans with the milk for a time. The stomach of

a 55-day seal contained milk and a few *Euphausia superba* and other crustaceans. Another pup . . . 2 months old, was filled with *Euphausia*, with a few fish eyes also, but no milk. Fish is the usual adult food, but crustaceans are much more easily caught by the young."

INCREASE IN WEIGHT OF THE PUPS

Lindsey (1937) states that the weight of the Weddell pup at birth is from 50 to 78 lb., and that the mean weight at birth of 17 pups was 64.1 ± 1.84 lb. Lindsey went to considerable pains to study the increase in weight of these pups from birth until the time of separation from the mother. Of the pups that he had marked by branding so that he could follow them through early life 18 (12 of them males), were weighed at frequent intervals "averaging oftener than once every third day". He provides a table, "which shows the mean gain in pounds for each of the first 6 weeks".

Lindsey's figures are more instructive when the "mean gain in pounds" is translated into percentage increase in weight in the course of the week, taking the mean weight on the day of birth as the starting point.

	MALES			FEMALES		
	Weight of animal in lb.	Gain in lb. in week.	Per cent. gain in previous week.	Weight of animal in lb.	Gain in lb. in week.	Per cent. gain in previous week.
Birth	64.1	—	—	64.1	—	—
End of first week	88.8	24.7	38.5	96.2	32.1	50.0
End of second week ..	125.7	36.9	41.5	134.8	38.6	40.1
End of third week ..	161.1	35.4	28.2	172.2	37.4	25.7
End of fourth week ..	192.6	31.5	19.5	200.7	28.5	16.6
End of fifth week ..	225.7	33.1	17.1	226.8	26.1	13.0
End of sixth week ..	249.8	24.1	10.7	250.9	24.1	10.6

When this is done the astonishing fact emerges that the male pup nearly, and the female pup actually, increase their weight by 50 per cent in the first week of life (see fig. 3). Then by the end of the second week of post-natal life the weight has increased to just double what it was at birth. Lindsey states (1907, p. 135): "The maximum recorded 7-day gains for 9 individuals follow: 35, 40, 40, 45, 46, 48, 49, 49, and 50 lb. Thus several seals averaged 7 lb. actual daily gain for 7 consecutive days or longer." After 6 weeks the difficulties of making regular measurement became greater owing to the increasing time the pups spent in the water. "At about the

seventh week the rate of gain diminishes rapidly until there is a cessation of weight increase, and a pronounced loss occurs. For example, a seal that weighed 300 lb. at 52 days of age, lost 17 lb. in the next 17 days . . . and another weighing 283 lb. at 36 days, weighed 245 lb. at 59 days. This reversal in weight change is correlated with the beginning of nutritional independence. It was not possible to follow any of the young sufficiently long to determine how soon the loss of weight was regained."

Through the courtesy of Dr. Lindsey the author was able to make use of certain of the original figures from the Ross Sea, and from these it has been possible to obtain the accompanying diagrams (figs. 4 and 5), showing the connection between,

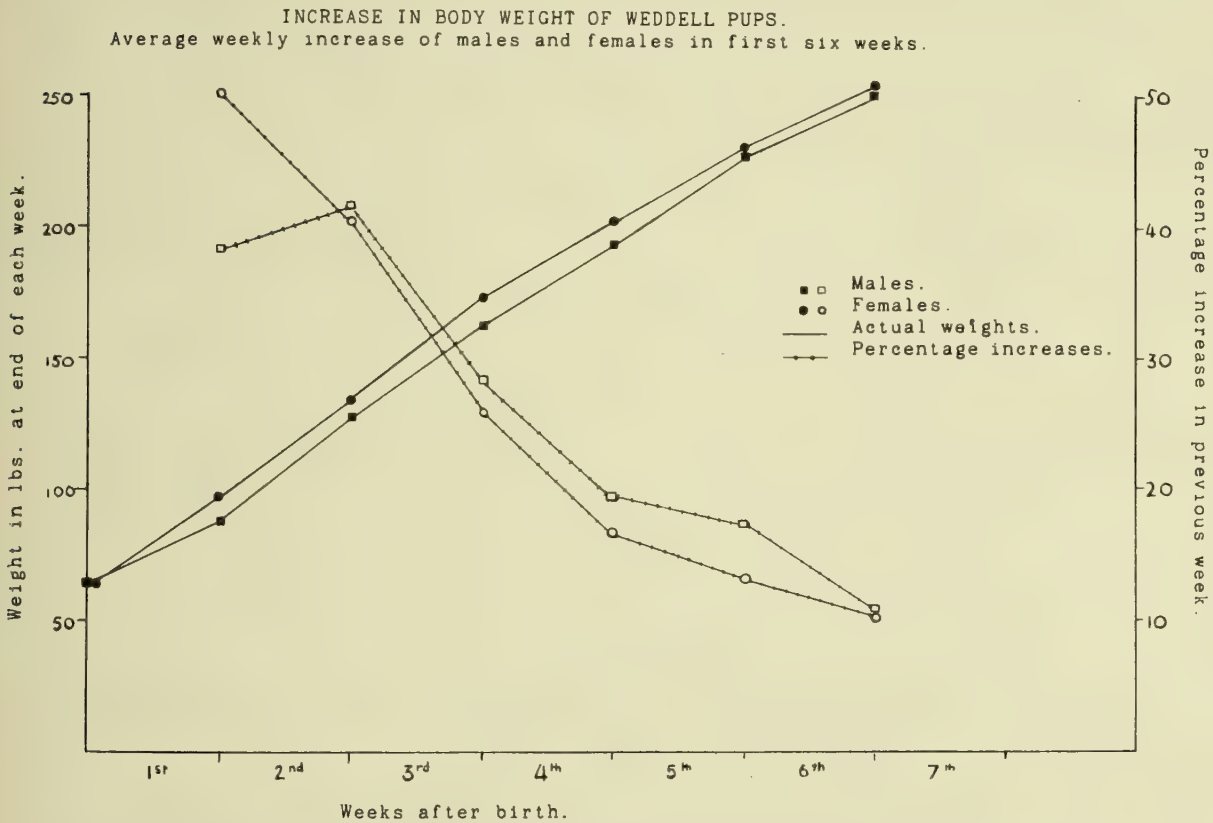


FIG. 3.—Diagram to show the average weekly increase in body weight of Weddell pups in the first 6 weeks of life, from Lindsey's figures from the Ross Sea. The percentage increases in weight during each week are also shown.

and the increase in, weight and body-length in these first few weeks of life. In the diagram (fig. 5), a few figures of Bruce's (1915) from the South Orkneys are included. It is clear that the very great variations in size between individuals appear at an early age. For example, a male pup measured by Lindsey at the age of 27 days (230 lb. and 68 in. long) is even at that age a trifle bigger than a young animal measured by Bruce (220 lb. and 67½ in.) that was about 270 days old. The weight difference may simply be the expression of that decrease following the end of lactation already remarked upon by Lindsey.

In *Otaria byronia*, Hamilton (private communication) states that there is a visible decrease in size of the pups after weaning. Likewise, Fraser Darling (in his

book of essays, *A Naturalist on Rona*) states that the pups of the Grey seal treble their weight at birth during the four weeks of lactation, and that there is little apparent further growth for 9 months.

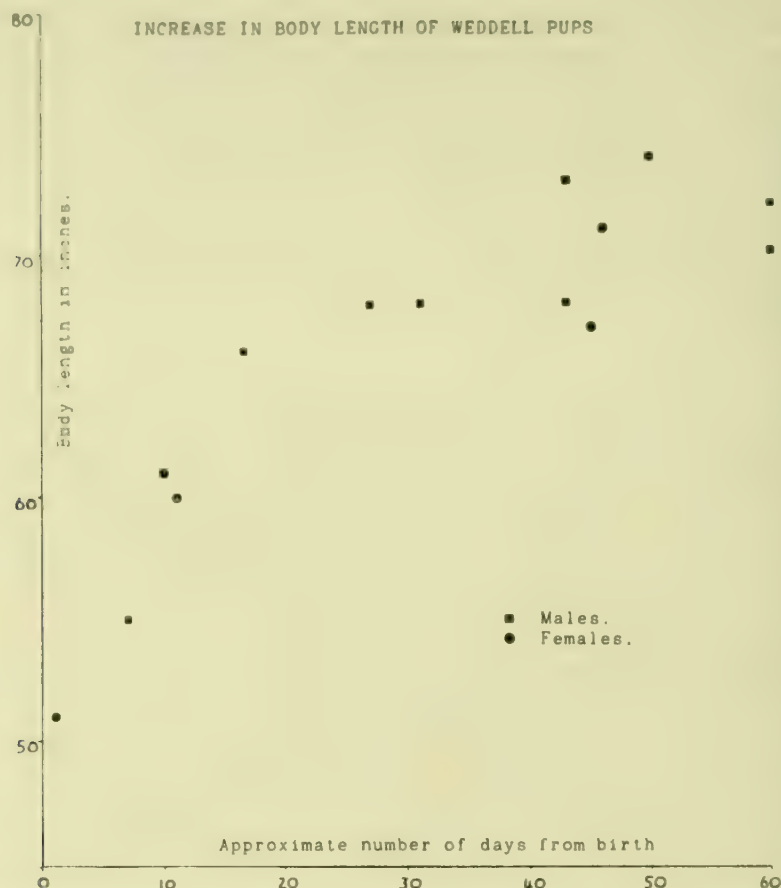


FIG. 4.—Diagram to show the increase of body length of Weddell pups during the first 2 months.
(Compiled from Lindsey's manuscript notes.)

WEIGHTS OF THE ADULTS AND BLUBBER THICKNESS

Very few actual measurements are available of the weights of adult Weddell seals. Bruce (1915) gives the following list of weights of animals from the South Orkneys. (Here are included only those of his seals that were more than 80 in. in length.)

Male	12/7/03	100 in.	787 lb.	(Blubber 250. Skin 80. Carcase 457 lb.)
Female	2/9/03	110 in.	838 lb.	
Female	21/9/03	c. 110 in.	920 lb.	(Bruce gives measure- ment as 124 in. from nose tip to rear margin of hind foot.)
Female	24/9/03	115½ in.	908 lb.	

Lindsey (1937), in the Bay of Whales, found the weights of one or two adult Weddells. He states (p. 137): "A mid-winter female collected in July . . . was estimated to weigh 900 lb. It had a layer of blubber 4 in. thick" and it is probable that this "constituted well over one-third of the total weight of this 110-in. seal. Yet the skin and blubber of a 112-in. female taken in December just after rearing its young weighed only 170 lb., or 55 per cent of that of the July female . . . and its total weight was only 597 lb."

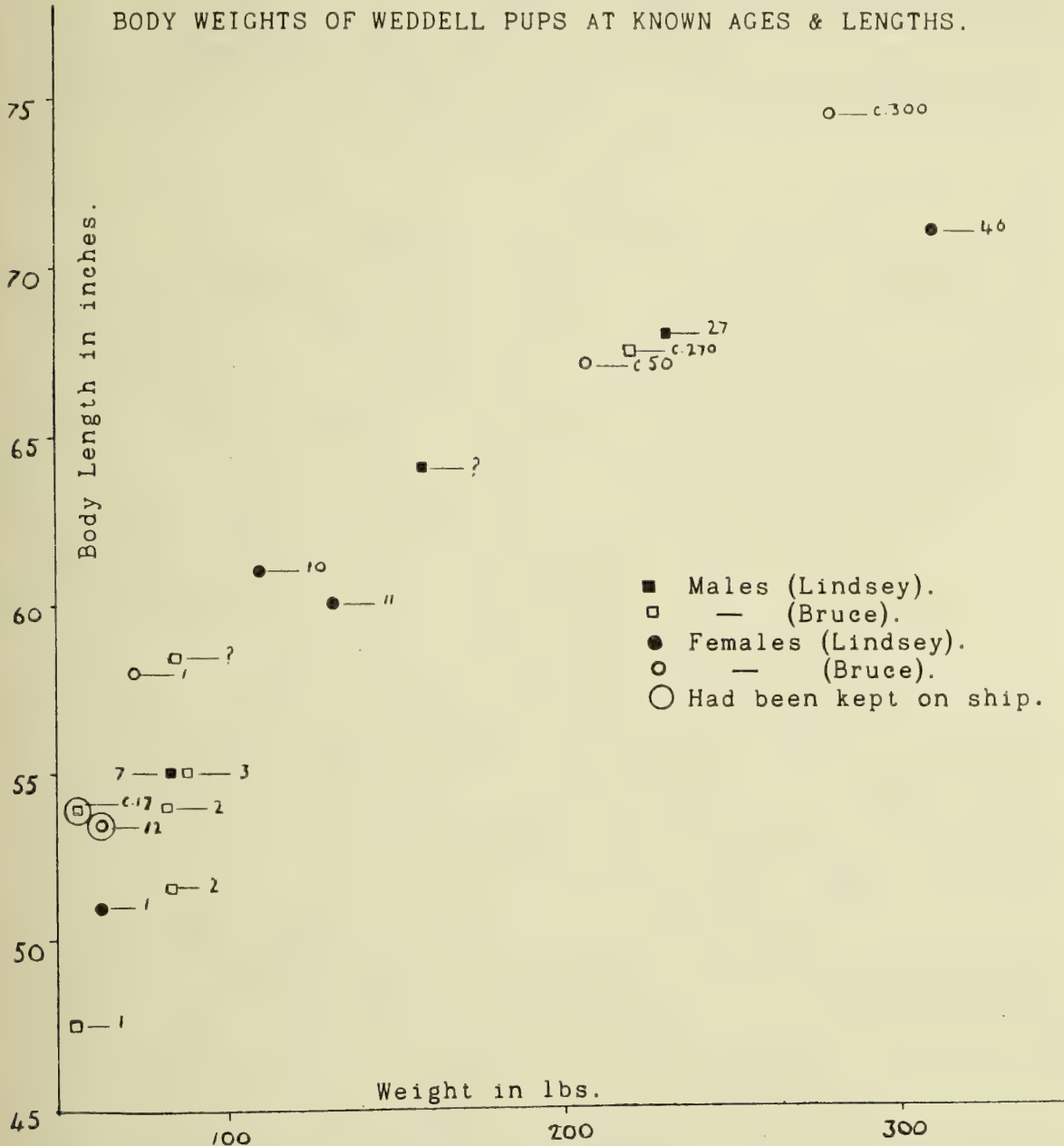


FIG. 5.—Diagram to show both the increase in weight and the body length of Weddell pups of known age in days. (Compiled from Lindsey's manuscript notes.) The sexes are shown separately. A few figures from Bruce (1915) are added, some of his animals having been kept for unspecified lengths of time on the ship before death.

In Graham Land it was not possible to make any complete weight determination of adult seals.

The blubber in the Weddell seal is of approximately the same thickness over most of the body, but is thinner towards the limbs and head. The thickness of the layer over the body varies during the year from about $1\frac{1}{2}$ in. to somewhat over 3 in., being thickest in the females during the winter, before the pupping. After parturition the blubber is called upon as a food reserve in the production of milk for the pup in its first few weeks, and consequently diminishes greatly in thickness, as does the weight of the entire animal. The blubber thickness and total weight of the males exhibit no such marked fluctuations, but the blubber is usually thinner at about the New Year, when the breeding season is ending and the moult is beginning.

GROWTH AND AGE

POSSIBLE METHODS OF AGE GROUPING

To study the composition of a wild population it is clearly necessary to be able to distinguish between the members of the two sexes, and to assign a fairly accurate age to the individual animal. Among some mammals the sexes are clearly distinguishable by size or form of the body, or by particular secondary characters. In the Weddell seal, however, there are no such obvious distinctions, and the two sexes are so similar that in life unless the ventral side of the body is seen, the males and females usually cannot be distinguished. With practice one comes to associate a somewhat more scarred appearance with the males and the largest size with the females. These criteria are quite inadequate in life to make complete distinctions, and observation of the ventral side is always needed. As to the division of the population into year groups, in certain of the larger mammals this is simple, at least with the younger groups, on general appearance, size, hair colour and condition, antlers, teeth, or otherwise. In other mammals splitting into year groups has not so far been found possible, partly owing to the overlap between groups by great individual variations, or through lack of observations on large enough numbers. In the Eared seals, it is possible to distinguish with fair accuracy by general appearance between the age groups of the Alaskan Fur seal (Allen, 1880; Elliott, 1881; Osgood, Preble and Parker, 1914), and Hamilton (1934), claims a like success with the Sea Lions of the Falkland Islands.

Osgood, Preble and Parker, (1914, p. 59), state: "For practical purposes there are seven classes of male seals (i.e. of the Fur seal of the Pribilof Islands), and four classes of females. The classes of males are the pups, the yearlings, the 2-year-old bachelors, the 3-year-old bachelors, the 4-year-old bachelors, the 5- and 6-year-olds or half-bulls, and the bulls or males of 7 years and over. The classes of females are the pups, the yearlings, the virgin cows or 2-year-olds, and the bearing cows of 3 years and over. It is especially important to distinguish the bachelors of 2, 3, and 4 years, since they are the ones from which quotas and reserves must be taken. The other classes are mostly so easily distinguished as to require no special discussion." (p. 20): "Males and females, however, have approximately the same length of life, from 12 to 14 years", as shown by branding experiments. There seem to

be no well-authenticated records of the length of life of any Phocids, except in captivity (Flower, 1931).

In the Weddell seal such splitting up into year classes has been found quite impossible by general observations on the live animals, or by direct observations on the individual seals at death. All that it is possible to do is to separate off the youngest year group from the older seals, but even this may be difficult towards the end of the year, just prior to the birth of the succeeding group.

There are, however, a number of characters which may be helpful in attempts to separate the age groups, and these will now be considered in turn. It is to be remembered that in the Weddell seal, since all the pups are born within the same short period each year, the age of any individual in months is always a known number plus some exact multiple of twelve. That is to say that all Weddell seals killed in the same month in any year must either be of the same age or be separated in age by an exact number of years.

Apart from general appearance, which has already been stated to be of little value in the Weddell seal as a direct criterion of age, size (i.e. body length) is the most obvious character to study. So far as possible, every seal killed in Graham Land was therefore measured in a direct line from nose tip to tailtip. But the measurement of a large mammal is always difficult, and particularly is this so with seals. Observations in life of the seal moving along almost in the fashion of a loopercaterpillar show a bewildering apparent change of body length, and when the seal has been killed it is clearly a very extensible creature. If the individual has been shot in the head or neck it can easily be drawn out to a greater length than if it has been shot elsewhere, and the length of a seal always increases considerably if it be dragged along a beach or over ice before measurement is completed. The measurement of a seal, in the view of the present author, cannot be more accurate than ± 2 in., and the error may very possibly be more. This impossibility of accurate individual measurement must be borne in mind when attempts are made to separate year groups of seals on the basis of body length figures.

In addition to body lengths the appearance and size of the skull in many species of mammal is often found to be most helpful in attempts to divide the population into year groups. A series of male and female Weddell skulls was prepared, with this end in view, and details of the observations and analyses of the figures are set out in a subsequent section. Likewise in certain mammals, the whales in particular, observations of the ovaries have been of great value in elucidating female ages. The results of the observations made on the ovaries of the Weddell seal will be described shortly.

Of further possible methods of age determination in mammals, another, which has actually been of use among seals, is observations on the claws. Plehanoff (1933), working with the Harp seal, has studied certain ridges on the claws, finding those of the fore-limbs more clearly marked than those of the hind-limbs. He found that the pups have one ridge on the claws, the 2-year-olds have two, and believes that there is an annual ring added with increasing age. He gives a table showing in parallel columns for 10 seals 'length of claws', 'length of body', 'length of skull' and 'supposed age'. He thinks that the same method of age determination is applicable to the Bearded seal, and likens this claw growth to that of certain 'Carnivores'

(unspecified). Observations on the claws of the Weddell seal were not made by the present writer, and whether such could be of use in attempts to determine individual ages in this species is unknown. For the Elephant seal, Wilson (1907, p. 56) remarks: "The nails show no signs of wear and tear, but have the appearance of having grown in water, though with transverse ridges indicative of periodic fluctuations in their growth."

Havinga (1933), working on the Common seal in Dutch waters, found that the *os penis* might be of some assistance in determining the age of the males. The bone increases rapidly in size towards the end of the third year of life; but his estimate of the third year is a deduction from the body length measurements. Hamilton (1939) has also made some use of the *os penis* in the Leopard seal where he found it to undergo a sudden enlargement in the third year, when he believed the animal to become sexually mature. The present writer unfortunately was not aware of such possible use of the *os penis* as a criterion of age until after the completion of his work in the field.

Three main possible methods of age grouping in the Weddell seal thus remain to be discussed, namely the body length, the skull form and dimensions, and the ovaries.

BODY LENGTH

Detailed knowledge of growth rates and ages, both average and maximal, in wild populations of mammals is extremely scanty, apart from the recent studies of various species of whales in the Southern Ocean. This remark for mammals as a whole is likewise very true for the Pinnipedia, a group that has been much neglected. Much more work has been carried out, however, on the Eared seals than on the True seals, the spur for further investigation having been the need to 'farm' the stock of Fur seals at the Pribilof Islands by the U.S. Department of Commerce and Fisheries. Likewise, Hamilton (1934 and 1939) has studied the growth and age of the stock of Falkland Island Sea Lions, and Lindsey (1937) has made an investigation of the growth of the Weddell seal in the Bay of Whales, based on the killing of 233 seals between 9 February and 17 March 1934. Lindsey's is the only detailed published work on the growth and age of a species of True seal. Havinga's (1933) figures for the Common seal are of far less value than they might have been, owing to no distinction being made between the sexes.

Osgood, Preble and Parker (1914), speaking of the Northern Fur seals and of their division into the year groups already mentioned, state (p. 59): "furthermore the standard of distinction adopted has been the one subject to the least variation, namely the total length of the animal. It has long been recognized by zoologists and students of classification and variation that the total length measurement of mammals is the most constant and reliable one that can be taken."

In the present paper full use is made of Lindsey's figures, and the author is also much indebted to him for his kindness in supplying further information and original figures beyond those appearing in his published work. Certain of Lindsey's figures for the Weddell seals of the Bay of Whales, being complementary to the author's series of measurements, are here reproduced for convenience and contrast.

First an attempt must be made to compare the body lengths attained by the male and female seals. Lindsey (1937, p. 128) remarks that "in computing mean length, the season's young, about 4 months old and less than 77 in. long, were omitted. The mean length of the 93 males over 13 months old was 94.12 ± 0.46 in., while 124 such adult or adolescent females averaged 96.46 ± 0.45 in. The difference in the mean length of the sexes therefore was 2.34 ± 0.64 in. Since this difference is 3.7 times its probable error, it appears that there may be a significant difference favouring the females. There were 15 females larger than the largest male."

A value for mean length can only be helpful for determining whether the males or the females of a species tend to possess the greater length, when it is certain that the populations on which the figures are based are truly comparable. For the figures to be truly comparable the samples which compose them must have the same age-group compositions. In the present instance there is no assurance on this point; it is not known whether the total male and female Weddell populations are alike in age-group composition nor even whether the samples bear the same relationship to the two sex populations respectively. As already explained, much of the doubt arises from the fact that all sampling of the Weddell population depends upon killing the animals when they are out of the water, and the lying out habits of the two sexes are by no means necessarily, and indeed often certainly are not, the same. The present writer therefore claims that Lindsey's figure of 2.34 ± 0.64 in. for the difference in mean length of the sexes, though possessing a mathematical significance relative to the two groups of seals actually measured by him, is without real value so far as the complete Weddell populations of the two sexes are concerned. A correct figure for the difference in the mean length of the sexes can only be obtained when it is possible either to sample the populations direct with complete assurance, or to make up samples for comparison from individual males and females of known age. At present it is impossible to do this.

Lindsey's last statement that "there were 15 females larger than the largest male" has, however, a precise meaning. He goes on to speak of the seals taken by the *Scotia* Expedition (1937, p. 129): "At the South Orkneys, Bruce (1915, p. 166) collected 6 adult males and 11 adult females, the maximum nose-tail lengths being 104.5 and 115.5 in. respectively. Of his 17 specimens, 5 females were larger than the largest male." (As already pointed out, in the author's opinion the length of a seal cannot be measured with greater accuracy than ± 2 in., and working to fractions of an inch in the initial measurements is in no way justified.)

In the Graham Land series of Weddell seals the largest male was 110 in. and the largest female 115 in. Of males over 100 in. in length there were 2 at 103 in., 1 at 104 in., 1 at 106 in., and 1 at 110 in. Of females over 100 in. long there were 3 at 103 in., 5 at 104 in., 2 at 105 in., 2 at 106 in., 1 at 107 in., 1 at 108 in., 1 at 109 in., 5 at 110 in., and 2 at 115 in. Thus, there were 7 females equal to or larger than the largest male at 110 in., and whereas there were only 5 males over 100 in. long, there were 22 females exceeding this length.

It is quite evident that in all three areas, the Ross Sea, the South Orkneys, and Graham Land, there is a well-marked tendency for the largest female Weddell seals to surpass the largest males in body length.

Lindsey's attempt to separate the age groups is based on the measurements

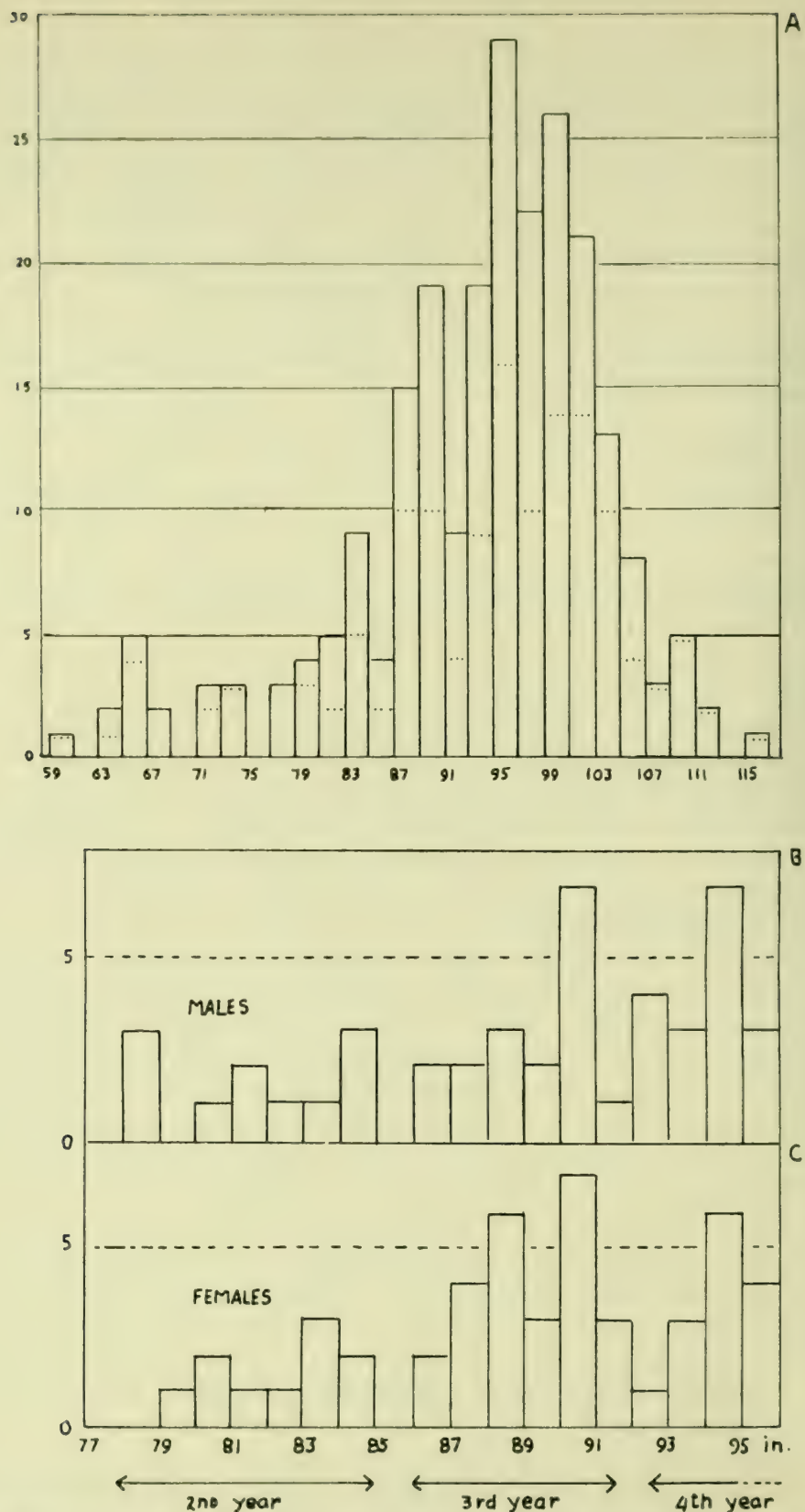


FIG. 6.—Reproductions of Lindsey's (1937) figs. 1 and 2, the original legends being: "Fig. 1. Frequency distribution of nose-tail measurements of 233 Weddell seals measured 9 February to 17 March. Class interval, 2 in. Males above the dotted lines; females below. Ordinate, numbers of animals; abscissae their lengths." "FIG. 2.—Frequency distribution of seals in their second, third, and fourth years, measured 9 February to 17 March. Class interval 1 in."

provided by the killing in the Bay of Whales of 233 seals between 9/2/34 and 17/3/34. Figure 6 is reproduced from his paper.

Lindsey (1937, p. 129) states: "The data [in fig. 6] enables us to define the annual age groups in terms of size for adolescent seals of different ages. Since all the young of each season are born within about one month, and the period during which we

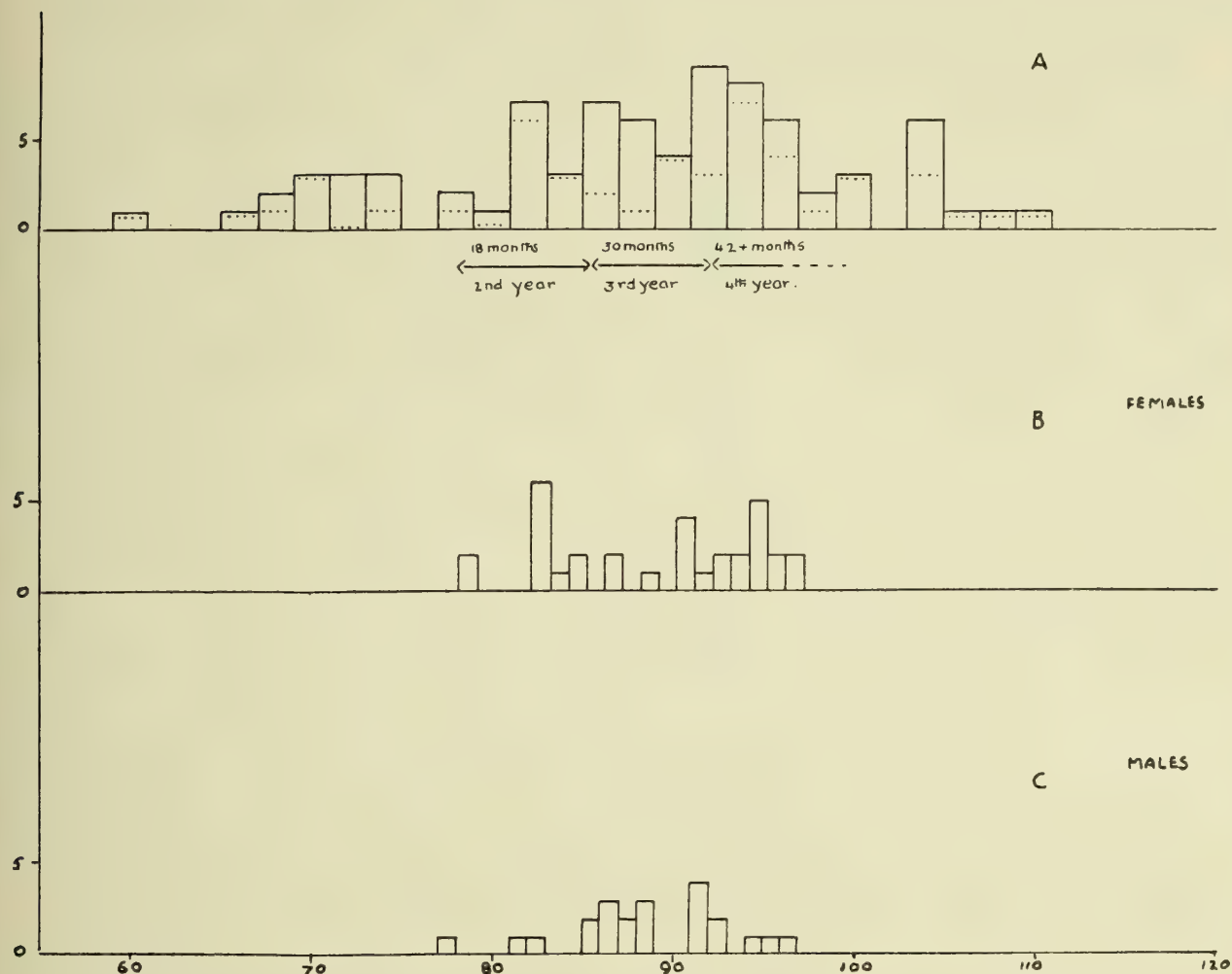


FIG. 7.—Diagram to show the frequency distribution of body lengths of male and female Weddell seals killed in Graham Land between 9 March and 21 April. This figure is directly comparable with Lindsey's (see fig. 6) except that here are included a smaller total number of animals and the killing was one month later in the year. Lindsey's suggested distinctions of year classes is inserted precisely as in fig. 6.

measured seals was similarly restricted, these frequency distribution charts show a drop to or toward the base-line between adjacent annual age groups. Their interpretation has been supplemented by field observations, skull data, and the skin series."

"The two smallest females that contained embryos were 87 in. long. Other small pregnant females measured 88, 89, 91, 94, and 95 in. Fig. 6 indicates that the very youngest pregnant seals are in their third year. This establishes the fact that the

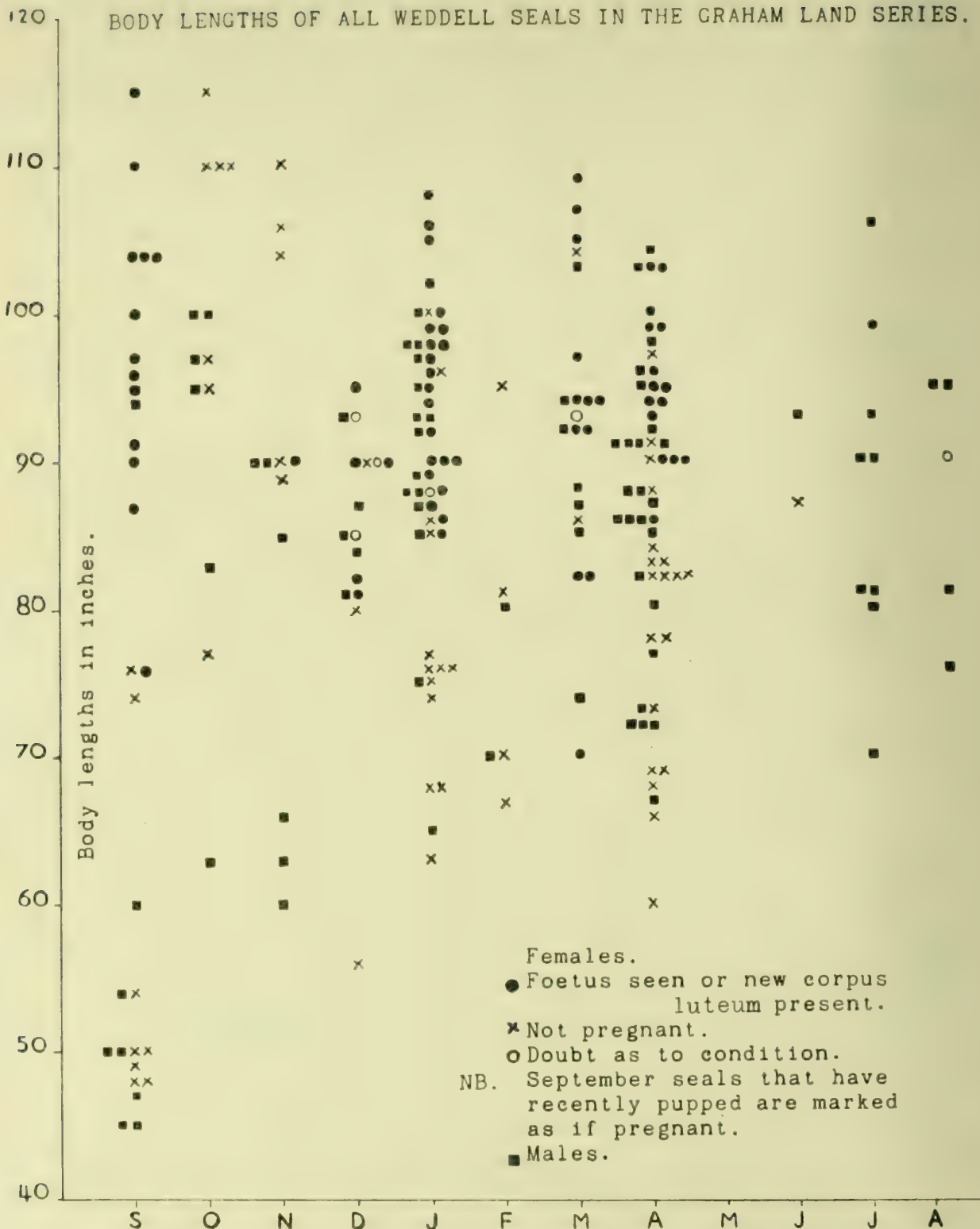


FIG. 8.—Diagram to show the body lengths, month by month, of all male and female Weddell seals killed in Graham Land. Distinction is made between the various classes of females

female when 2 years old has reached sexual maturity and may mate, gestation occurring during its third year, and the first parturition when it is barely 3 years old."

Thus Lindsey, working on the Weddell seals in February–March in the Ross Sea, found that the distinction between 4 months and 16 months seals at about 77 in. was clear, and he also found that the distinction between the 16-months non-pregnant seals and the 28-months (or more) pregnant seals came at about 85 in. His tentative point of separation between the 28-month (third year group) seals and those older lies at about 92 in. The separation points by body length of the 4, 16, 28 months and older seals Lindsey found to be almost exactly the same in both sexes.

The Graham Land seals measured are about the same in number (225) as those of Lindsey, but are spread over many more months, so that the number killed in any one short period is much smaller. Whether the Ross Sea and the Graham Land Weddell seal populations behave in their growth in precisely the same way is not known, but this may be assumed for present purposes. For comparison with Lindsey's figures, 81 Weddells killed in Graham Land between 8 March and 21 April in two separate years are set down in the same way as his figures for 233 seals killed a month earlier in the year (fig. 7). Since in the Ross Sea the Weddell's pup about a month later than in Graham Land, Lindsey's seals are effectively about 2 months younger than the Graham Land seals with which they are here being compared. It will be seen that in a general way the figures for the Graham Land seals correspond with those from the Bay of Whales. The difference between the first two groups is fairly distinct, but that between the next two much less so. The number of measurements is, however, small, which may largely account for this lack of distinction.

The above method of setting out the available figures is not altogether satisfactory, but has been adopted simply for the purpose of comparison with Lindsey's diagrams, these being limited to seals killed in a single month. To make use of all the figures available of the Graham Land seals, a more satisfactory and illuminating method of setting out the data is possible. The individual body lengths of all the seals can be set out month by month (fig. 8), and likewise this may be repeated over the months of several succeeding years, treating the sexes separately (figs. 9 and 10). When this has been done any regular growth trend in the population should be apparent. The males and females are treated separately, and a distinction is made between the pregnant and the non-pregnant females (and those females doubtful in this respect).

In the diagrams so produced (figs. 9 and 10), tentative 'average' growth curves have been drawn in, from which it seems that the males tend in the early stages to grow rather more rapidly than the females, despite the fact that in the end the females reach a rather larger size than the males. It is also clear that, starting at an early age, there is a large amount of individual variation in size among seals of the same age, and that this variation soon swamps the distinction between the year groups; so soon in fact that no certain distinction can be made even as far as an age of about 2 years. It is clear, however, as Lindsey (1937) had already found, that impregnation of the females takes place normally when they are just over 2 years old. There is a suggestion that possibly one or two of the females may have become pregnant at the age of only 14 months, unless these small seals in reality represent particularly dwarfish 26–30 months old animals. 'Dwarfishness' in seals is not

BRITISH GRAHAM LAND EXPEDITION

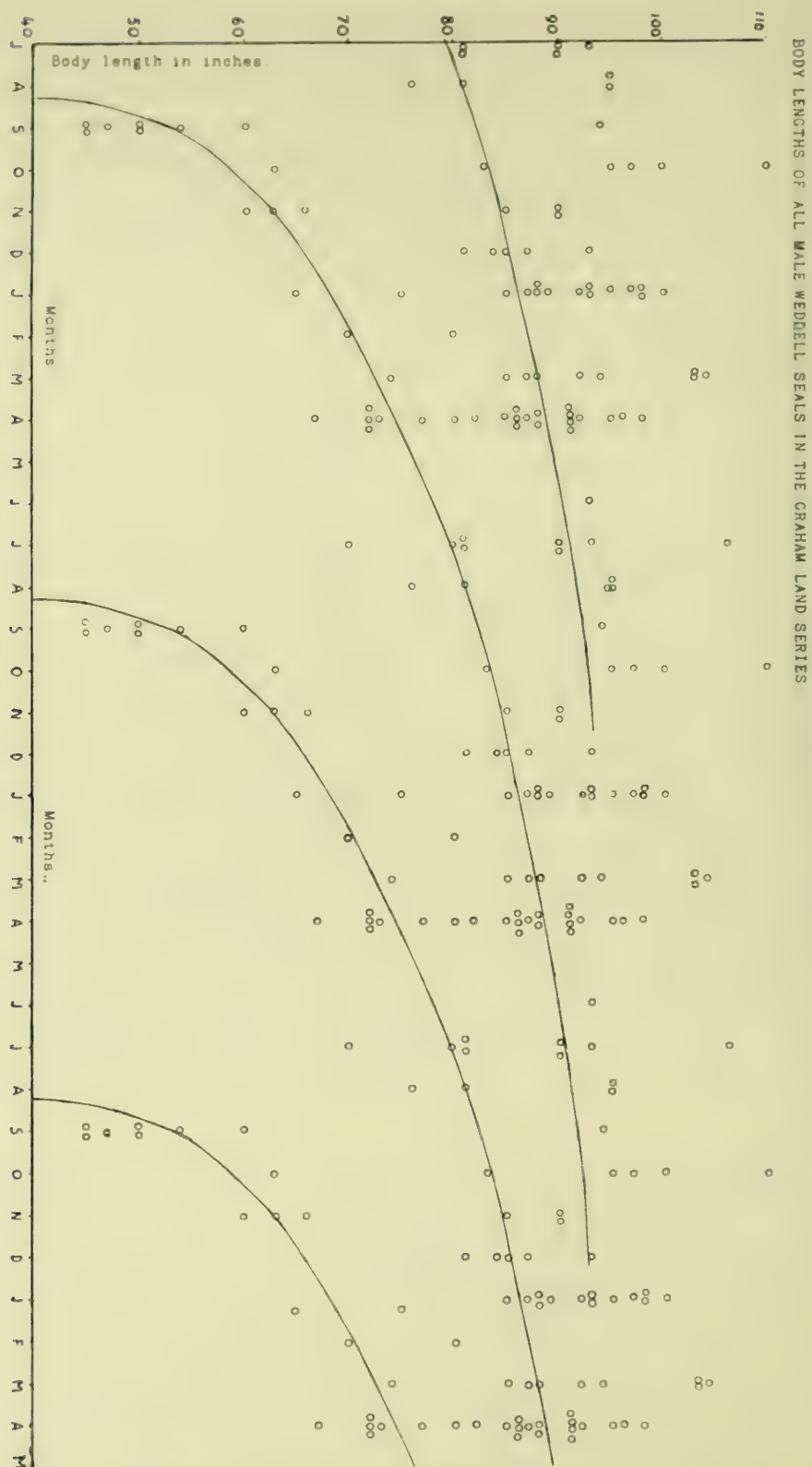


FIG. 9.—Diagram to show the body lengths of all male Weddell seals taken in Graham Land, repeated month by month over several years to show the most probable method of growth.

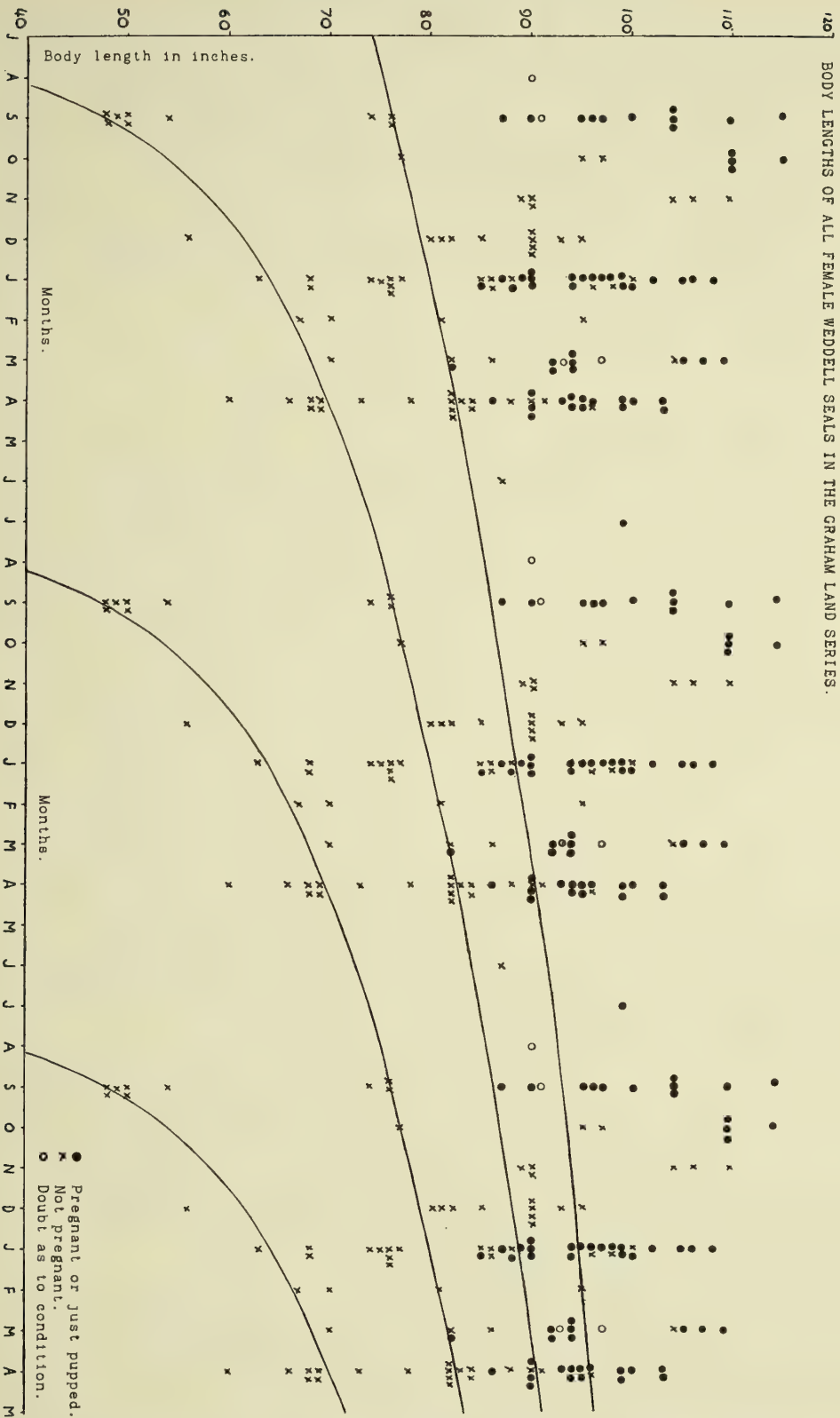


FIG. 10.—Diagram to show the body lengths of all female Weddell seals taken in Graham Land, repeated month by month over several years to show the most probable method of growth.

unknown, for Nansen (1925) and Wollebaek (1907), speak of dwarfed Fjord seals (*Phoca foetida*) that have been carried away from their normal feeding grounds near the coast and thenceforth pick up a precarious existence in the pack ice.

Thus beyond the middle of the second year it is not possible certainly to separate the age groups of the Weddell seal, or to determine the age of an individual, from either general observations on the animals alive or dead, or from the body length, owing to the magnitude of the individual variations in growth. An attempt is therefore made in the next section to see if more satisfactory results as to age determination can be made from examination of the skulls.

SKULLS

(a) *Sex Differences in the Skulls*

The first point to arise in the consideration of the skulls of Weddell seals is that of sex distinctions. In various mammals of several groups it is easy at once to distinguish between the male and female skulls. For example, among the deer, cattle, and horses, sex distinction is easy. Likewise among the polygynous Otariids and in the Elephant seal, in all of which there is sexual disparity in size, the distinction between the male and female skulls is very obvious. In the Walrus too (Allen, 1880) there is apparently in most instances a fairly well-marked distinction, the tusks of the female being both longer and more slender. In the view of some workers it should be possible, in any species of mammal, with practice and a long series of skulls, to class every individual one as definitely male or female. From his work on the Weddell seal the present writer cannot subscribe to this view. He believes that in many species of mammal where there is no well-marked sexual disparity in size and behaviour, although it may be possible to distinguish the more feminine from the more masculine skulls, in a proportion of the skulls it will not be possible to sex with any certainty. This is the state of affairs in the Weddell seal, where with practice it has been found possible to pick out from a series certain skulls that are definitely those of males, and likewise certain others that are female, but about half of the total it has not been found possible to sex with certainty.

With the Sea Lion of the Falkland Islands, Hamilton (1934 and 1939) found no difficulty in separating the male from the female skulls, and in a polygynous species such as *Otaria*, where there are great size differences between the adults of the two sexes, his finding was to be expected. His practised eye was able in the present series of Weddell skulls to suggest certain points that were male or female trends, but these trends and others have not proved enough to do more than separate the 'advanced' skulls of either type.

The following characters have proved of some use in attempts to distinguish the male and female skulls:

- (a) The nasal opening as seen from the front tends to be more laterally compressed in the female.
- (b) The nasal opening viewed from the side tends to be less vertical in the female.
- (c) The anterior part of the face tends to be less massive in the female, and

when viewed from above presents a rounder aspect, while in the male this dorsal aspect is more square.

- (d) The jugal process of the squamosal tends to be less expanded distally in the female and to curve less sharply upwards, while in the male it tends to expand, and the general curves of the zygomatic arch are more marked in the vertical direction.
- (e) The basisphenoid in the female tends to be less hollow antero-posteriorly, and is laterally less elevated than in the male.
- (f) The mandible of the female tends to be less massive, especially anteriorly.

The form of the mandible and the basisphenoid seem to be a little more reliable than the other characters. The conclusion cannot be escaped that given a series of unsexed Weddells skulls it would be possible to pick out with confidence a few that were certainly either male or female, but no more. It would not be possible to give an accurate diagnosis of the sex of many of the series, and given a single skull it would be possible to give it a reliable sex in less than 50 per cent of cases. On the other hand, given a series of skulls all of the same, but of unknown sex, it would be easy to determine that sex.

Working with the Leopard seal, where the sexual disparity in size (in favour of the female) is better marked than in the Weddell, Hamilton (1939) points out that the characters distinguishing the sexes are subject to a considerable degree of individual variation, but in spite of it, it is possible to sex well-grown skulls, but with juvenile specimens it is difficult and often impossible, at any rate in the present state of knowledge.

(b) *Skull Dimensions and Proportions*

Even a first glance at a series of Weddell skulls shows one very plain fact: all the skulls are remarkably similar in general appearance. On closer investigation it is seen that in finer detail there is much individual variation, but the general similarity, despite variations in over-all size, remains clear. In neither sex of the Weddell seal is there any well-marked maturity series. There is no marked change in skull outline or proportions, nor increase in size of crests or tuberosities with age. Nor in this species of seal can the teeth be of much help in fixing the age of the individual. The milk dentition is reabsorbed in utero, the pup is born with the permanent set partly cut, and the whole series is functional within a few weeks. Later in life, the cheek teeth being simply grasping organs, there is no regular rate of wearing down, the wear in fact being very slight. An indication of age may sometimes be obtained from the state of the canines and incisors (second upper incisors and canines in particular) which are gradually worn down in the process of ice-sawing in winter. On the other hand the amount of wear so produced will vary with the locality in which the seal has wintered, depending on whether it was necessary to saw much ice and whether this was spread over a few or many months. Likewise, Chapsky (1936) states that in the Walrus, where the tusks are used in obtaining the food, the amount of wear is not exclusively an indication of age.

Both in the present series of skulls (54 female and 32 male), and in Lindsey's

series, the number available for examination is much smaller than the number of body length measurements. But counteracting this lesser amount of material is the fact that a skull can be measured with an accuracy not possible with the seal's body as a whole, where a minimal error of ± 2 in. is probable.

Lindsey (1937, p. 132) gives tables showing the distribution among his skulls of condylo-premaxillary lengths by 10 mm. class intervals, and zygomatic widths at 5 mm. intervals, treating the males and females together. His tables are reproduced below:

LINDSEY'S TABLE I

DISTRIBUTION OF CONDYLO-PREMAXILLARY LENGTHS OF 59 SKULLS. CLASS INTERVAL 10 MM.

Length in mm.	170-179	180	190	200	210	220
No. of skulls	1	4	2	6	5	2
Age	4 days	1-10 days	10 days	16-45 days	43-(60) days	(60-140) days

Length in mm.	230	240	250	260	270	280	290
No. of skulls . .	0	2	7	10	12	7	1
Age	—	(15-29) months	(27 months upward)				

LINDSEY'S TABLE II

DISTRIBUTION OF ZYGOMATIC WIDTHS OF 71 SKULLS. CLASS INTERVAL 5 MM.

110-114	115	120	125	130	135	140	145	150	155	160	165	170	175	180
1	5	3	3	3	4	2	3	8	5	5	12	8	7	2

Lindsey (1937, p. 131) points out that, with certain specified exceptions, all the skulls considered were obtained in the autumn months of February and March. "When arranged in order of size, the autumn skulls, therefore, might be expected to show several marked discontinuities between the several age groups of adolescent and pre-adolescent seals. Of four skull dimensions measured in this series, frequency distributions of the two most significant are given. . . . For many of the first year skulls [i.e. up to 6 months old] the age is known to the day. The figures in parentheses are estimates based on skull characters, nose-tail measurement, and date of collection. A marked break occurs in both the length and width curves, falling at the same point in the series for both measurements. All skulls under 225 mm. long and 142 mm. wide are season's young [i.e. up to 6 months old] whose nose-tail length did not exceed 74 in." His previous figure "shows a corresponding hiatus at the 75-76 in. interval, separating individuals less than 6 months old from those born one year before them. But between the latter and the third-year skulls no such clear separation is found. Growth in length has lessened in its rate, and individual variation contributed to the overlapping. It seems probable, however, that the second

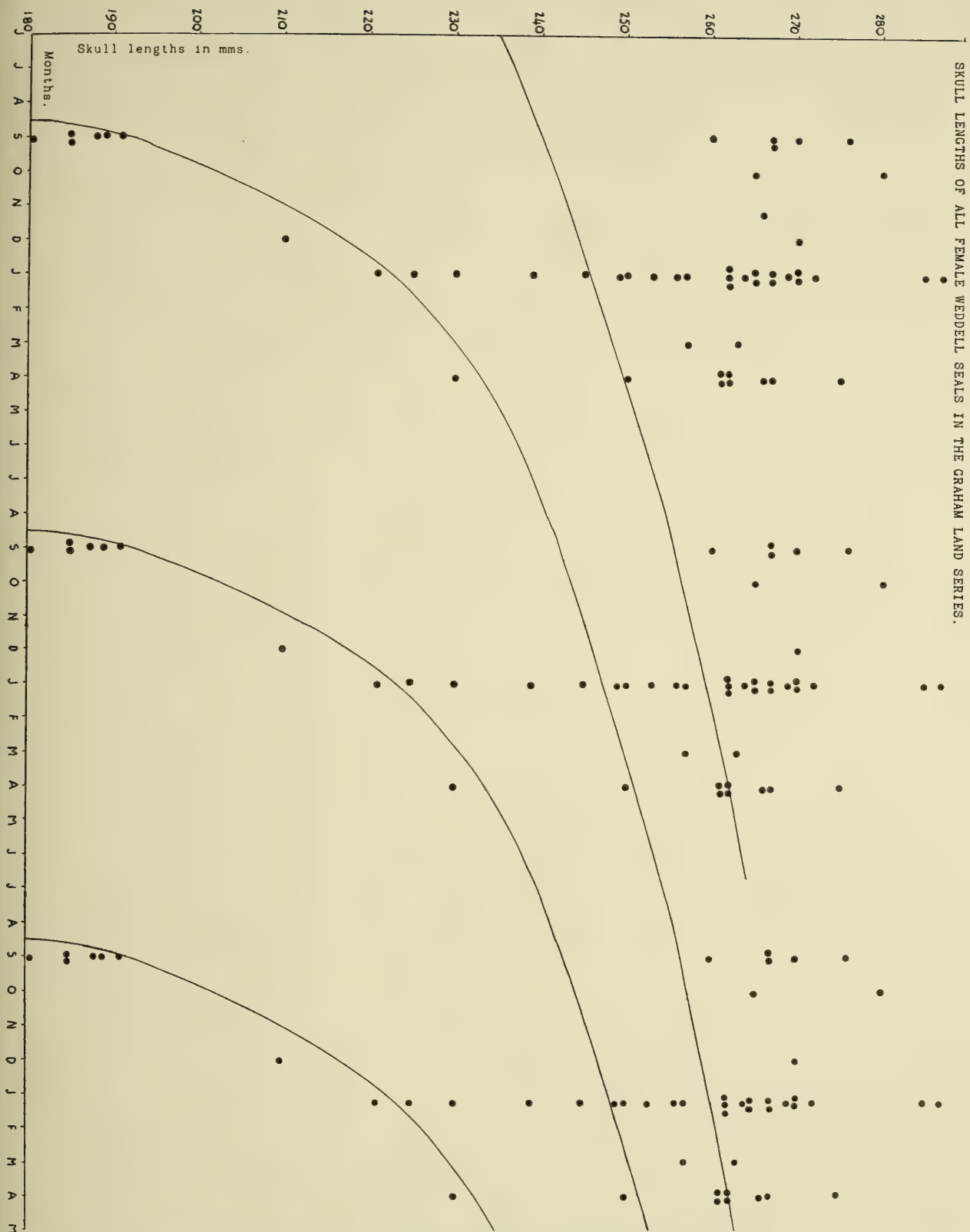


FIG. 11.—Diagram to show the skull lengths of all female Weddell seals repeated over the months of several years to show the most probable method of growth.

No. 1 (*d*)



FIG. 12.—Diagram to show the skull lengths of all male Weddell seals taken in Graham Land, repeated over the months of several years to show the most probable method of growth.

division between age groups falls in the 250-mm. rather than the 260-mm. class. . . . Skull data furnished no evidence for setting off the third-year group from the fourth." Thus Lindsey finds from his series of skull measurements that the separation of the Weddell seal into year groups has at best been advanced no further than his previous tentative division on the basis of nose-tail lengths.

With the Graham Land skulls (as with the Graham Land body measurements), owing to the date of death not being confined to a single period of the year, it has not been possible to set out the data in the same way as has Lindsey (1937). Instead, the skull lengths (PMX to hind border of condyles) of the two sexes separately have been plotted individually against the months of several years set out in succession (figs. 11 and 12). By this means an indication of the general rate of increase in skull length during the first 18 months or 2 years of life is provided, but beyond that point, just as with the body lengths, individual variations swamp all distinctions between the year classes.

Though there would seem to be a great variation in skull length between Weddell seals of the same age, it is possible that some other character, such as general skull form or extent of closure of the sutures, might be more helpful as a direct measure of age (i.e. separation of year classes). An attempt in this direction has been made, but without success, despite the series (of 54 female and 32 male skulls) ranging in both sexes from day-old pups to the largest seals found. As already pointed out, even a cursory glance at a collection of Weddell seal skulls brings out the point that, as a whole, all the skulls are remarkably similar to one another, but that in detail there is an immense individual variation, a small skull for example having a certain suture closed and a large one having it still open.

The skulls of Weddell seals under 18 months of age (as judged from the body and skull length curves) are obviously those of young animals, but beyond that it is not easy in some instances to determine with certainty even whether a skull is 'young' or 'old', so great may be the variations between skulls of the same length and the same sex. Apart from the first 6 months or so, when the fore-part of the skull is clearly growing at a greater speed than the cranium proper, there is no directly apparent alteration in proportion of the various skull dimensions with increasing total size. Attempts to find any such regular changes in proportion have been made, still in the attempt to determine individual ages or to split the material up into year groups, skull dimensions being plotted relative to one another and to body length and so on.

Comparison of body and skull lengths of individual seals (fig. 13) shows a *pari passu* growth (the coefficient of correlation for males is 0.746, for females 0.907), though there may be as much as 40 cm. difference in body length between seals with skulls of the same length. There is a tendency for the males to have a slightly larger skull at any given body length. The skull length shows a general tendency to decrease in proportion with increasing body length (as would be expected for all vertebrates, the head being greatest in proportion early in life).

Skull breadth in both sexes seems to be somewhat variable, with a small general tendency for the breadth to be proportionately greater in the larger skulls (fig. 14). The correlation coefficients for skull breadth and length are 0.531 for the males, and 0.873 for the females.

A comparison of skull weights with skull lengths likewise shows considerable variations, but there is a tendency for male skulls in the larger sizes to be heavier than the female skulls of the same length (fig. 15). In both sexes skull weight in proportion to body length is very variable.

In the first few months the 'face' is elongated relatively to the hind part of the skull, but later the proportionate lengths of the fore-part and the hind-part of the skulls show no definite trend (fig. 16). In each case the forward edge of the basisphenoid in the middle line is taken as the fixed point separating the 'face' from the

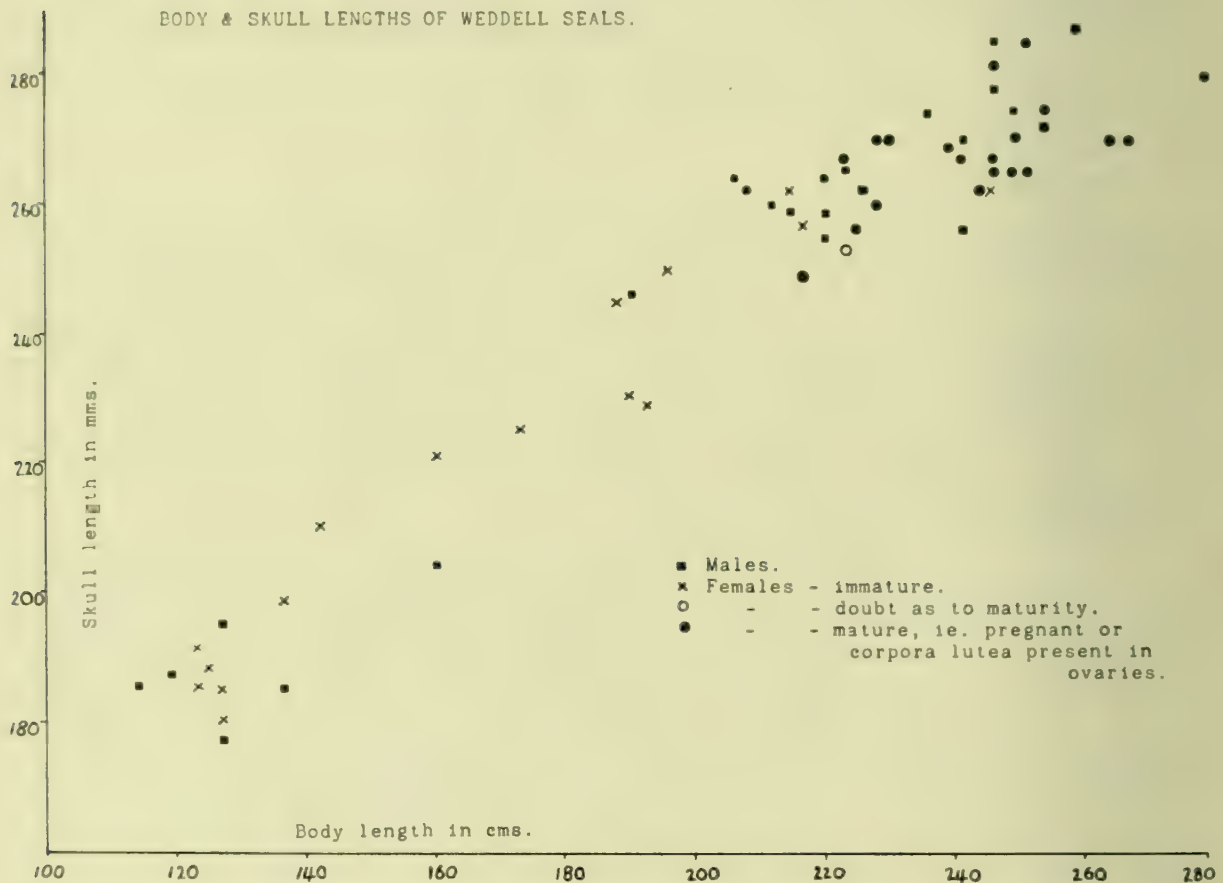


FIG. 13.—Diagram to show the relation between the skull length and body length of individual male and female Weddell seals from Graham Land.

hind part of the skull. Thus, as with the analysis of the figures of body length, a consideration of the skull dimensions and their relationships one with another and with the individual body lengths, etc., shows that there is no sufficiently well-marked change to make possible the certain determination of the age groups in either the male or the female Weddell seals. Certain trends are of course present, as is to be expected; for example, the skull length makes up a smaller proportion of the total length of the animal in the larger sizes. There is also a tendency for the larger or older skulls to be proportionately wider than those smaller or younger, and there is a tendency for male skulls to be a little heavier than female skulls of the same length.

In the absence of any marked age trends in skull dimensions, proportions or form (crests, tuberosities, etc.), attention is next directed to the state of closure or otherwise of the sutures themselves.

(c) *Sutures*

In a general way in mammals the closure of the various sutures of the skull is always an indication of age, but when a large series of skulls is examined it is soon

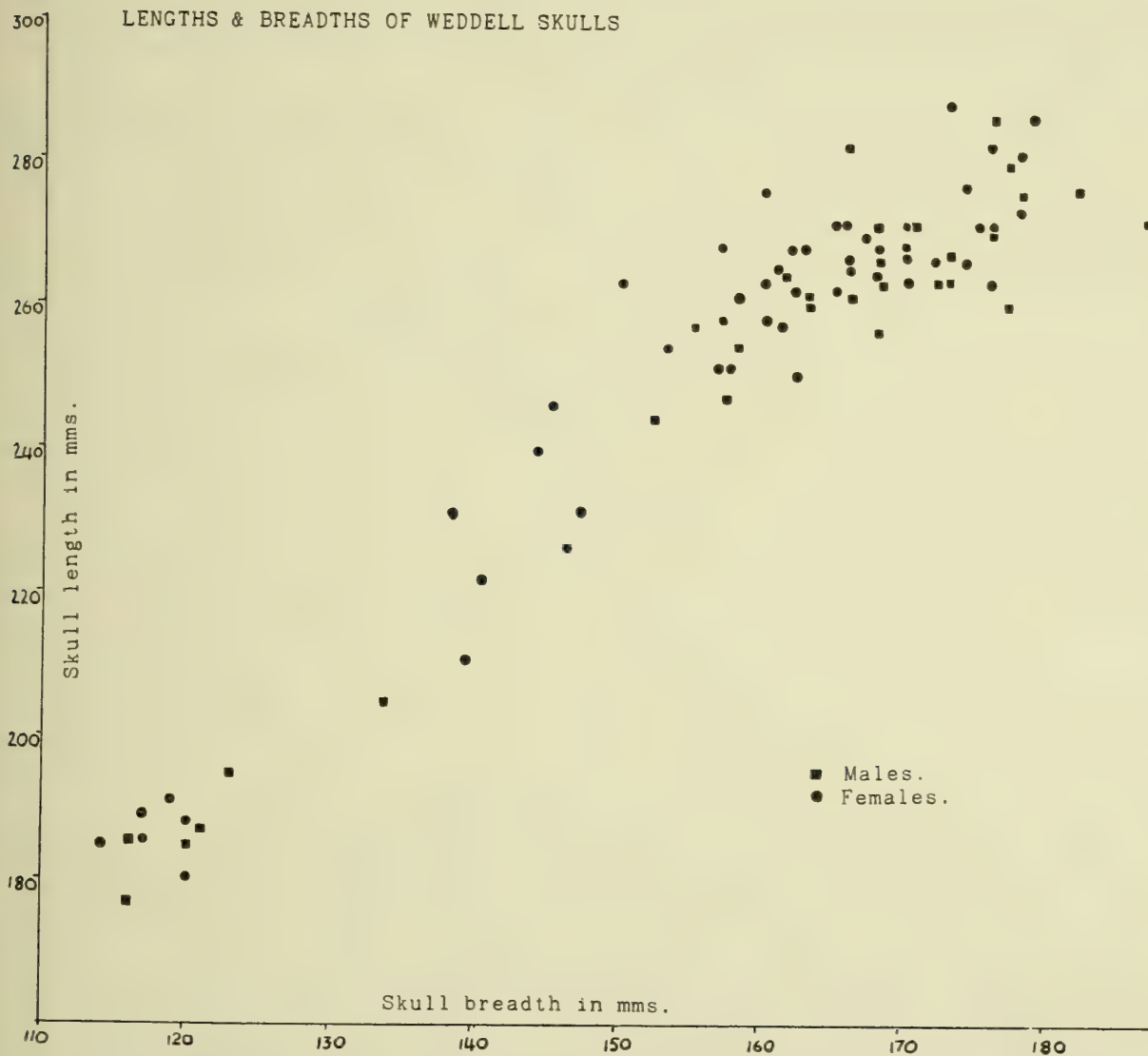


FIG. 14.—Diagram to show the relation between the skull length and skull breadth of individual male and female Weddell seals from Graham Land.

found that the rate of closure apparently may be very varied. A small skull may have many of the sutures closed, while a larger one may have many of them still open. In the Weddell seal this individual variation is well marked, so that the extent of closure of the sutures is clearly a character that must be used with caution, though

selected sutures may be very suggestive in determining the relative ages of different skulls.

The following is Lindsey's statement on the subject of the closure of the sutures (1937, p. 131-32). "The degree of closure of the sutures offers another general criterion of age. At 2 months the components of the brain case are still distinct, except for the occipitalia, which coalesce very early. The parieto-occipital suture is beginning to close at this time, the bones becoming firmly sealed during the first 6 months.

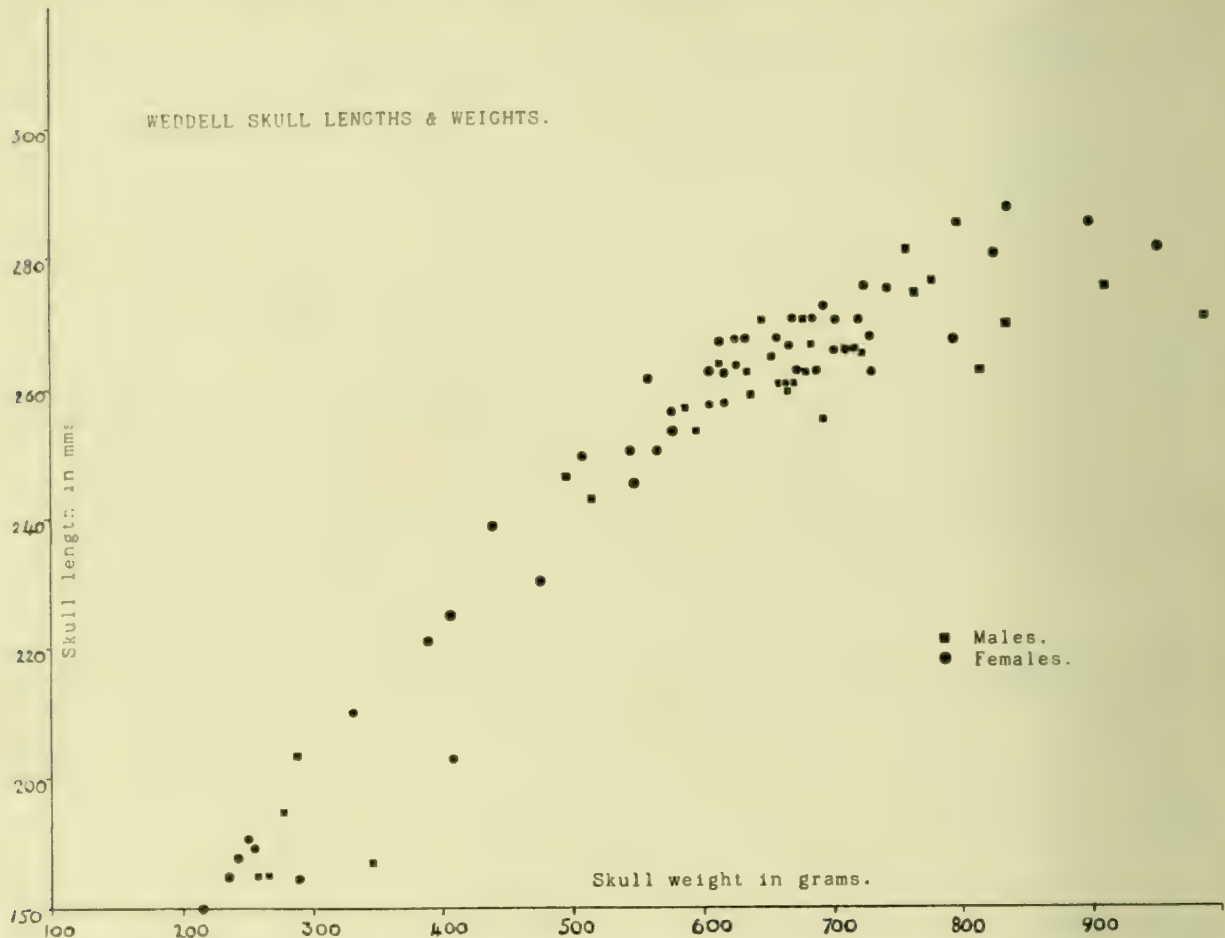


FIG. 15.—Diagram to show the relation between the skull length and skull weight of individual male and female Weddells from Graham Land.

Infrequently a conspicuous parietal foramen (10×4 mm.) persists throughout the second month. The second important suture to close is the parieto-squamosal, followed by the parieto-frontal, which remains conspicuous long after closing. In the 15-month skulls the parieto-squamosal usually is completely obliterated, with the parieto-frontal closed and sometimes almost disappearing. The basioccipital-basisphenoid suture usually remains well-defined in the second-year skulls but is largely closed in the third-year.¹ This probably is the best skull character for

¹ This statement is, of course, based on Lindsey's own estimates of age derived from the body length of the individuals from which the skulls came.

separating these age groups. Its closure begins medially, the lateral arms sometimes remaining open after complete obliteration in the centre.

The last sutures lost in the adult skull are the inter-maxillary, inter-palatine, and maxillo-palatines. This seems to furnish a much better indication of the age of adults than the skull length. Only one skull (282 mm.) shows closure of all three sutures . . ." Lindsey might with more accuracy have remarked 'indication of age' rather than 'of *the* age'.

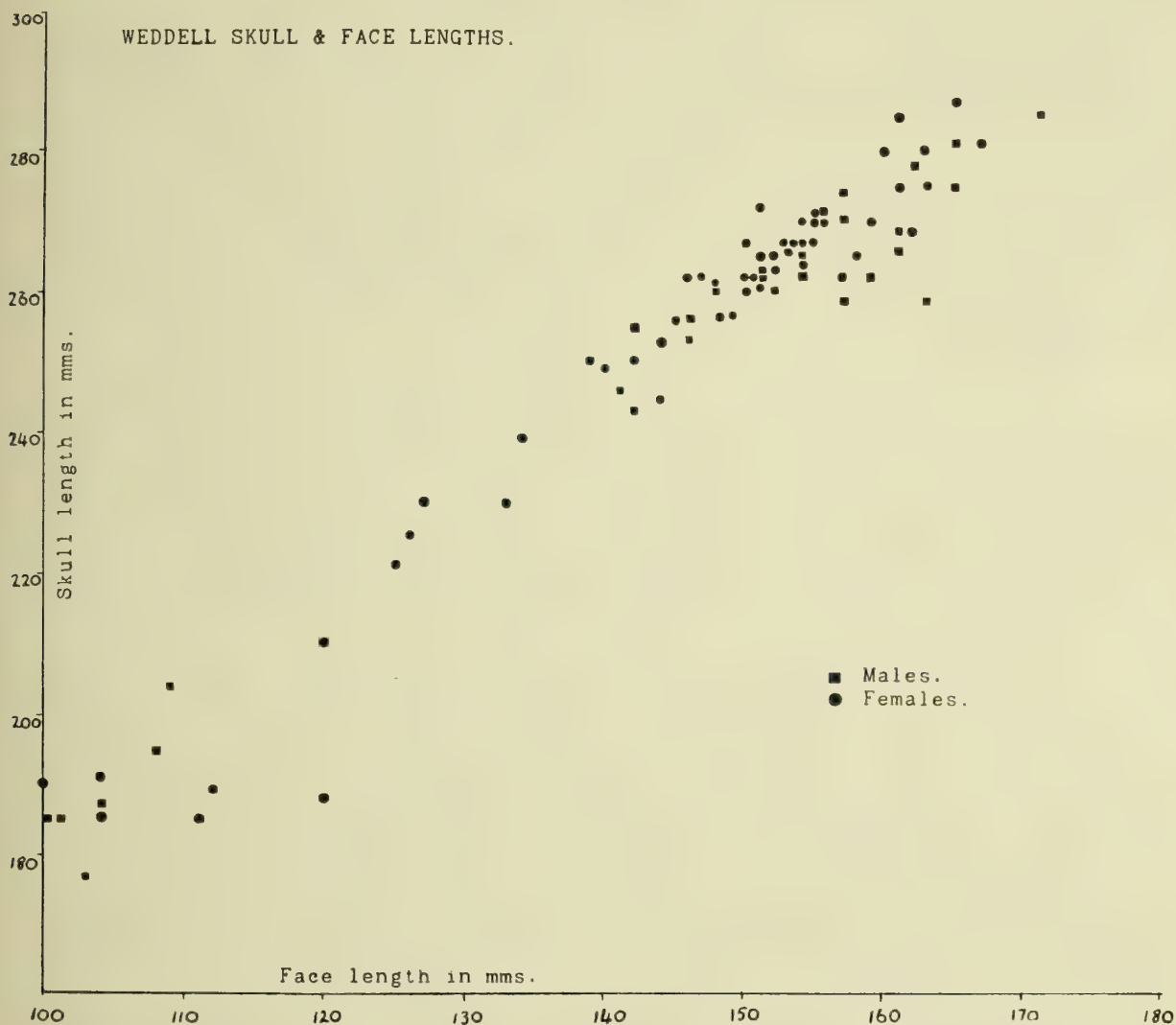


FIG. 16.—Diagram to show the relation between the skull length and face length of individual male and female Weddells from Graham Land. The 'face' length is measured forwards from the basisphenoid-presphenoid suture to the anterior point of the premaxillae.

Lindsey was able to follow many young seals through from birth until they were some months old, so that his remarks as to the closure of the sutures in the early stages are precise and are based on much more extensive observations than were possible for the present writer. The latter agrees with Lindsey that the sutures of the palate are among the last to close and that they may form a criterion of age

in the adult, but they do not, even in combination with other skull features, provide an actual measure of individual age.

This conclusion having been reached as to the impossibility of determining the age groups of the Weddell seal (beyond an age of about 24 months) from body or skull measurements or characteristics, or both combined, one is forced to turn to other possible methods of attaining this end.

THE OVARIES

(a) *Corpora Lutea*

One further possible method of determining the age groups is available, but for females only. This is the examination of the ovaries. These, as is explained shortly, are believed to be capable of giving a very fair indication of individual ages. In the Weddell seal normally each female produces a single pup when just 3 years old, and in each succeeding year. Evidence is brought forward to show that the number of corpora lutea persisting in each pair of ovaries is a direct measure of the number of pregnancies undergone. The individual age is therefore this number plus the two pre-adult years.

The evidence for this hypothesis of age determination must now be presented.

In recent years in the course of their investigations of the whales of the Southern Ocean, members of the *Discovery* staff have paid a good deal of attention to the ovaries. From the evidence there provided by the corpora lutea it has been possible to make important deductions as to the age of the animals concerned. The present writer has paid similar attention, though on a numerically smaller scale, to the ovaries of the Weddell seal, with somewhat similar results. The works of most importance in the present connection are those of Mackintosh and Wheeler (1929), Wheeler (1930), and Laurie (1937).

It is convenient first to outline the way in which mammalian ovaries in general may be of value in the investigation of ages: then the way in which they have been used in studying the whales and in which they may be used in the seals. The relative merits of whale and seal ovaries as sources of information may then be compared; and finally, the conclusions that can be drawn from the seals' ovaries and the detailed evidence on which those conclusions are based, will be presented.

In the mammalian ovary ovulation takes place at regular intervals. Each ovulation may be single or multiple, varying with the type of mammal. After ovulation the ripe follicle, having shed its contents, undergoes a remarkable development by which it is converted into a corpus luteum. If pregnancy does not supervene the corpus luteum soon regresses and a new ovulation will occur after an interval that may be long or short, according to the species. The corpus luteum of pregnancy may survive as a functional organ until parturition, or its effective life may be somewhat shorter. In either case it eventually regresses to become a small mass of scar tissue similar to the final state of the short-lived corpus attendant upon an unsuccessful ovulation. The subsequent history of the regressed corpus luteum (now more properly, but less conveniently for present purposes, known as a corpus albicans) is variable. In some mammals the corpora disappear more or less completely in the course of a few months. On the other hand, to take the opposite

extreme of a series, in certain mammals the corpora, though diminished in size, may persist even throughout the life of the individual animal. In such a case examination of the ovaries and counting the total number of corpora albicantia (i.e. old corpora lutea), would produce a figure that represented exactly the total number of ovulations that had taken place in the life history of the individual. Should it happen that the average total number of ovulations (both successful and unsuccessful) that have taken place per year is known, then obviously it would be possible to determine the probable number of years that the animal has been sexually adult. In a wild population where the sexual experience of the individual females is likely to be approximately the same, sometimes it may be possible to provide this average figure for the total ovulations per year. Then, if a sample of ovaries be examined and the old corpora lutea counted, a fair estimate could be made of the age composition of the female population.

This general outline may serve as a background for the consideration of what is found in the Weddell seal, and for comparing the seals with the whales that have been so extensively studied. It is apposite at this point to quote certain passages from the summaries to the papers on whales already cited, so as to indicate the lengths to which it has been possible to go with those animals. Mackintosh and Wheeler, (1929, p. 468) remark: "It is a peculiarity of the ovaries of these whales that the corpus luteum formed at each ovulation persists in a recognizable form for a very long time, probably for years, with the result that accumulations of old corpora lutea give some indication as to the number of ovulations which may have taken place. Other conclusions to be drawn from the reproductive organs relate to the determination of sexual maturity and the progress of the sexual cycle throughout the year." Wheeler (1930, p. 418), speaking of Fin whales, states that: "... physical maturity bears little relation to length, but is found when more than 15 corpora lutea are present in the ovaries. All ovulations are permanently recorded in the ovaries. Because whales act collectively the number of ovulations before pregnancy tends to be the same in any one season, and this manifests itself in the greater frequency of certain numbers of corpora lutea than others. Each peak of the frequency graph represents an age group at an interval of 2 years from the one previous to it." (The Fin whale normally breeds in alternate years.) "There are three peaks in the frequency graph before the physically immature whales give place to the mature. This indicates that physical maturity is attained when whales are from 6 to 8 years of age." Laurie (1937, p. 267) says: "The onset of physical maturity in Blue females coincides with the accumulation of 11 corpora lutea in the ovaries. Length above 81 ft. is no guide to age. Blue females become physically mature at a minimum length of 86 ft., though many grow much beyond this length. . . . Whales from 78 to 81 ft., a group which there is reason to suppose is a year group of newly mature whales, are found with an average of 1.91 corpora lutea. There is evidence that in subsequent years the increment is 1.13 . . . A tentative correlation between age and number of corpora lutea is thus established. The results suggest that whales over 2 and under 3 years old are found with two corpora lutea; subsequently there is an increase of 11 corpora lutea for every 10 years." It has not, however, been proved directly as yet that the old corpora lutea in the whale persist throughout the life of the individual.

Now may be compared the relative merits of the seal data and material collected in Graham Land with that for the Blue and Fin whales that have served as the basis for such conclusions as those quoted above. The seal data are of course far less extensive: there are some 65 pairs of ovaries of the Weddell seal available for examination, while those of the whales amounted to many hundreds. Then the large size of the whales' organs greatly facilitates examination. Mackintosh and Wheeler (1929, p. 382) speak of the ovaries of the Blue and Fin whales in the following terms: "They are elongated bodies measuring usually between 20 and 40 cm., and differ from the ovaries of most other mammals in their highly convoluted condition and the prominence of the frequently numerous corpora lutea and follicles, which give the surface a very irregular appearance." They continue (p. 387): "In whales of all the species examined the corpus luteum of pregnancy is a very large and conspicuous body with a scar marking the point of rupture of the follicle. The scar, which is sometimes of considerable size, consists of a dimple about 5 mm. in diameter surrounded by a raised area which may be called the 'corona' and which may measure as much as 6.0 cm. in diameter . . ." The mean diameter of the young corpus luteum of pregnancy is more than 10 cm., while for a time after parturition it is still 5 cm. or more across. "Careful slicing of the ovaries reveals no traces of older corpora lutea which are not to be distinguished on the surface." (p. 391). It is clear that the ovarian constituents of the whale are on the grand scale. The far smaller dimensions of the seals' ovaries and their parts will shortly be apparent as will be the fact that the old corpora lutea (other than the most recent) in the seal are rarely to be located simply by examination of the intact ovary. The great advantage of the seal material compared with that of the whales lies in the far greater regularity of behaviour of the seals. The adult female Weddells in any one area all pup approximately at the same time, and pupping takes place at the end of the individual's third and each succeeding year. This regularity of behaviour clearly has certain advantages when deductions are to be made, but it has at the same time serious disadvantages during the collection of the material. The Weddell seals could only be killed when lying out on the ice or on beaches. Since their habits in this respect varied from month to month, there were considerable periods when no seals could be taken, and this, combined with the limits imposed by local ice and other conditions, resulted in the ovarian material being both less extensive and less well spread over the year than could be wished.

The evidence afforded by the present series of Weddell seal ovaries will now be discussed. As remarked above, the seals all tend to pup at the same time, there being a peak period within a maximum variation of about 4 to 5 weeks. It seems certain that the Weddell seals in the more northerly parts of Graham Land pup about 2 to 3 weeks earlier on an average than those to the south. This must be borne in mind in that the collection includes ovaries from various parts of the coast. In a wild population it is fair to assume that the period of gestation will not vary among individuals by more than a few days. Hence the bulk of the sexually mature females must be impregnated within a few days of one another. This takes place roughly at the end of November or the beginning of December, shortly after separation from the previous year's pups, which have by then been suckled for about 7 weeks. The seals pupping for the first time do so at the same time as their elders, so that they

too must have been impregnated within the same short period. Examination of the testicular material available shows that ripe sperm are present for some time before the end of November. It seems probable that the females, having pupped together, then begin to mature their follicles at about the same rate, and are then ready once more to take the males at about the same time. Since the animals are confined to the narrow coastal belt and the males are present throughout, it is probable that any one female will be served as soon as she is willing to accept the male. The time relation of the period of acceptance and actual ovulation is not known, but it is unlikely that they are other than approximately simultaneous. So it comes about that all the female Weddells must tend to ovulate at about the same time, and it is highly probable that as soon as they do so they will at once become pregnant. Cases of twinning are so rare as to be safely neglected in the present discussion. There can be little doubt that it so happens that the female Weddells produce but a single ripe ovum (each year), this giving place at once to a successful pregnancy. The small proportion of 'missed pregnancies' is discussed in a separate section.

Whether, in the event of the female failing to be served successfully, a second ovulation will occur is unknown. The carnivores as a family are typically monoestrous, though often multiparous. The slight variation in pupping time shows that should there be a second ovulation when the first has failed, this second ovulation must occur rather quickly after the first. A polyoestrous animal so large as the Weddell seal would be unlikely to have a period between successive ovulations of less than, say, 3 weeks. The maximum variation of pupping time, and therefore of successful ovulation time, is 4 to 5 weeks, so that should an ovulation fail to be succeeded by pregnancy, there is only time for a second ovulation within the limited period, if the first one was a little in advance of the average. The specific limit to the period during which ovulation can be successful possibly comes from the male side, or so the limited testicular material suggests. If it be the case that the failure of sperm supply limits the period during which pregnancies can be initiated, it is conceivable that the females might continue to ovulate without the chance of pregnancy supervening if the first one, or two, were a failure. Since the vast majority of the female Weddells do successfully become pregnant at the same time, the amount of material available that might demonstrate further ovulations is exceedingly small. It cannot therefore be definitely stated that such further ovulations never occur. A small number of other follicles may, however, reach a moderate size, even so much as 8 mm. in diameter, before undergoing regression.

Hamilton (1939) met this same difficulty in his work on the Southern Sea Lion. But with practice he found he could discriminate between pregnant and non-pregnant mature females without killing them, and thereby was able to make a special collection of material from which to work out the sexual cycle in the absence of pregnancy. He then found that cows could continue to ovulate outside the breeding season. The Southern Sea Lion can, in fact, be polyoestrous. But with the possibility of a very small number of unproven exceptions, it is clear that the great majority of the female Weddell seals ovulate only once, and that successfully, in each sexual season (i.e. once per year).

We can now trace the consequences in the ovary of a successful ovulation; that is to say, we can follow through the life of the corpus luteum of pregnancy. The

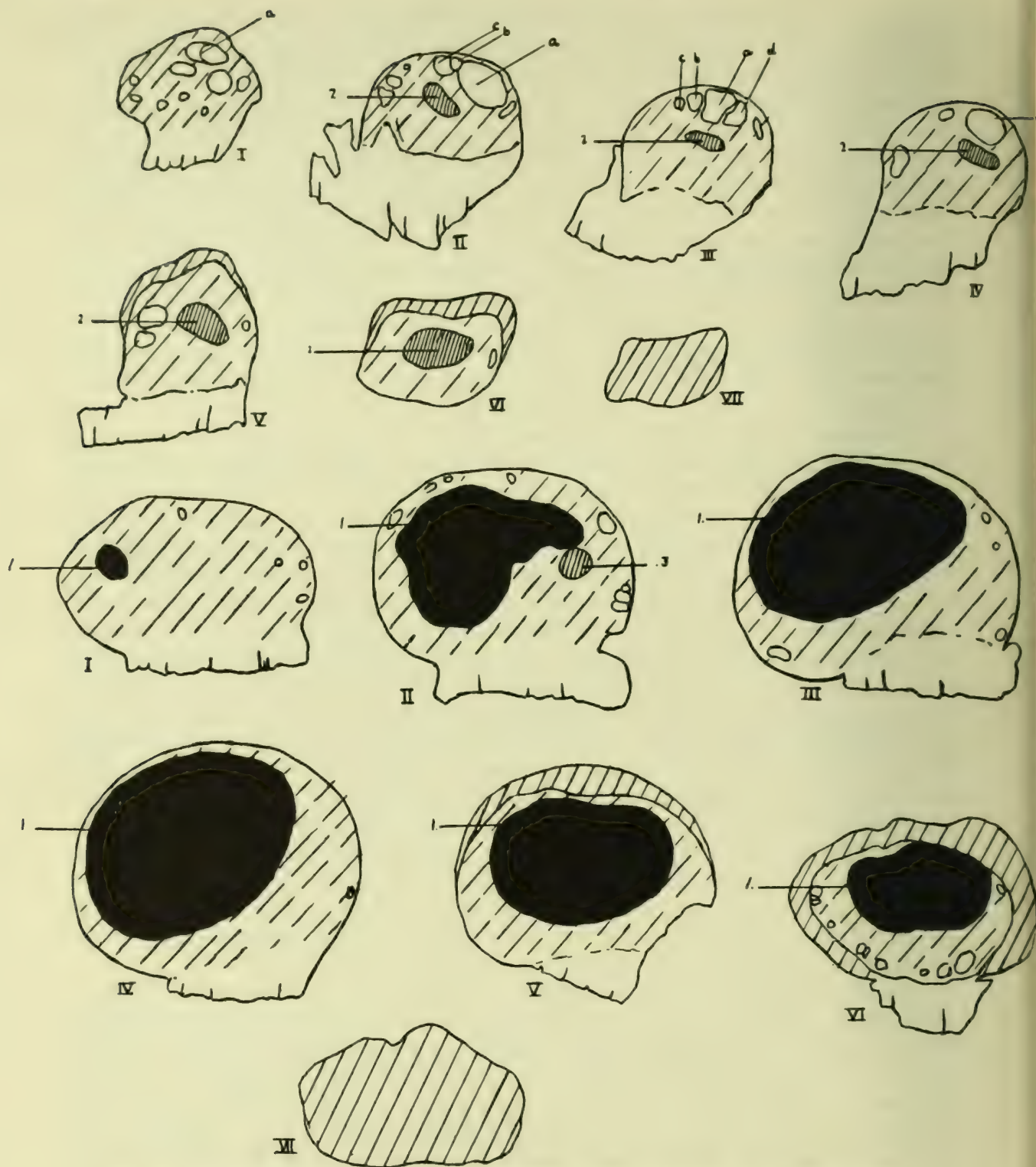


FIG. 17.—Ovaries of 105-in. Weddell seal, Debenham Islands 14/3/36. Three corpora lutea are marked 1, 2, and 3; No. 1 being in connection with a 25-cm. foetus. The sections average $\frac{3}{16}$ in. in thickness. Drawings $\times 1$.

corpus luteum of pregnancy in most mammals seems to develop extremely rapidly, reaching almost to its full size within a very few days. In the Weddell seal the fully-developed corpus luteum, which tends, like the ovary itself, to be ellipsoidal in form, has an average greatest axis about 25 mm. in length. This corpus luteum maintains its full size throughout pregnancy and then rapidly decreases in size after parturition. Examination of the ovaries of lactating seals shows that ovulation does not take place until this period (about 7 weeks) is complete, but then follows quickly. Ovulation usually takes place in the opposite ovary to that containing the recently functional corpus, and the foetus lies in the horn of the uterus on the same side as the ovum was shed. The ovaries of lactating seals always show one corpus luteum, that of the recent pregnancy, still of considerable size, and much larger than any other old corpora that may be present. This recently functional corpus luteum of pregnancy, besides being smaller in size than it once was, is already much harder and more fibrous in texture than during gestation.

The other old corpora lutea must now be considered. The old corpora lutea are discrete small masses of scar tissue, often deeply embedded in the general ovarian stroma, and certainly not, as in the whales, projecting as knobs upon the surface or at least determinable therefrom. The number of these old corpora lutea (corpora lutea b. in the nomenclature of the whale investigators) in the Weddell seal is never great. In but 7 seals are there more than a total of 5 corpora lutea, including the functional one of pregnancy (if any). Since in all probability each seal ovulates only once each year, any accumulation of old corpora lutea must necessarily be slow.

The numbers of old corpora lutea found on sectioning the ovaries in the collection may now be considered. When the old corpora are shown graphically (fig. 18) in relation to the body lengths of the seals from which they came, certain features are clear. It is seen that there is a general tendency for the longer seals to possess a greater number of old corpora lutea:¹ there are variations and exceptions, but the tendency is clear. Now the length of a seal must be some indication of its age, despite the variations in individual growth rates. Therefore, apart from all other considerations as to the possible number of corpora produced each year (which in actual fact is believed normally to be one only), it is apparent that there must be some connection between the number of old corpora and age. It is evident that the old corpora lutea are very persistent, but so far there is no direct proof as to whether or not they eventually disappear completely. Evidence on this point may, however, be obtained from a consideration of their frequency distribution. If all the old corpora remain permanently visible and countable in the ovaries, it would be expected that there would be progressively fewer seals possessing each number of them as the scale is ascended. Alternatively, if the old corpora gradually diminish in size and disappear after a fairly standard number of years, there would be a tendency for a certain number of them to be more 'fashionable' than any other number. That is to say, it would be expected that all seals over a certain age would tend to have the same number of corpora visible, since the first formed ones would be already disappearing. At the same time very few, if any, seals would have a greater number of old corpora than this most fashionable number. Examination seems to show that

¹ There is a positive correlation coefficient of 0.426; this is 'highly significant'; it would occur by chance in less than 1 per cent of cases.

the former alternative is correct and the latter incorrect. Therefore it can safely be assumed that the old corpora lutea persist as long as the seal lives.

This persistence may be compared with Hamilton's findings in the Southern Sea Lion. He states (1939, p. 135): "Corpora lutea disappear fairly rapidly; in the

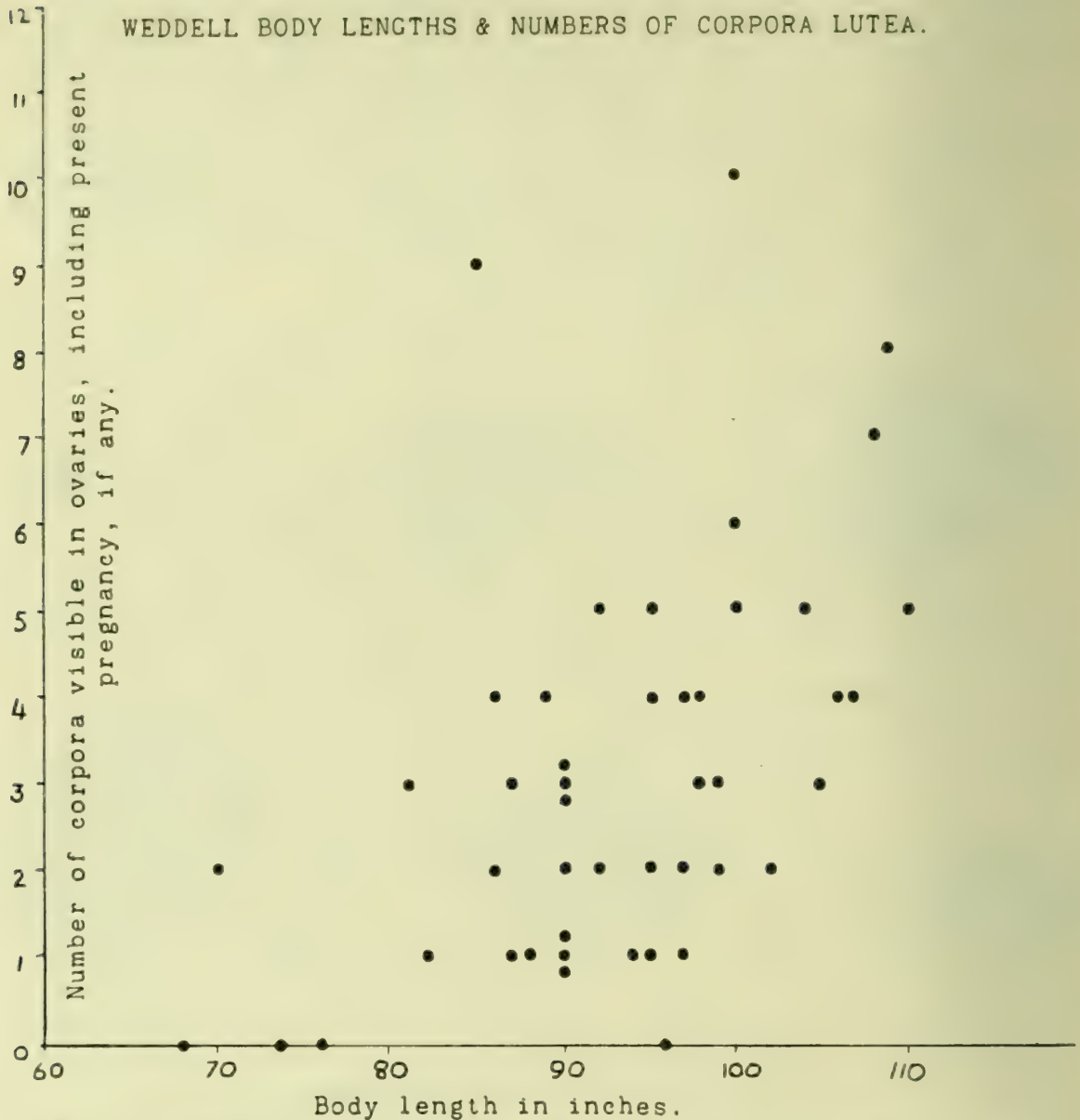


FIG. 18.—Diagram to show the relation between body length and the numbers of corpora lutea in the ovaries of Weddell seals in the Graham Land series.

whole series 2 are present in but 6 cases and in only 3 others can the traces of a third be found."

The suggested proof of the persistence, in the Weddell, of the old corpora lutea from their frequency distribution, may be made more clear by an example. Imagine a population in which there are 631 adult females and that their age distribution is

such that there are 100 females in their first year of adult life (i.e. pregnant for the first time), 95 in their second, 90 third, 85 fourth, 80 fifth, 70 sixth, 60 seventh, 40 eighth, 10 in their ninth, and 1 animal now pregnant for the tenth time. This is the type of age distribution that one would imagine to exist in such a population. Now consider three possible cases: (A) the corpus luteum from every pregnancy persists throughout the life of the individual; (B) each corpus luteum exists as a recognizable entity for 5 years exactly; (C) the lives of the corpora lutea are somewhat variable, one-third of them lasting 4 years, one-third of them 5 years, and one-third of them 6 years. The frequency distribution of the numbers of corpora lutea that will occur in this population (of 631 mature female Weddells with age-distribution as set out above) will then in the three cases, A, B, and C, be approximately as follows:

CASE A

*Actual No. of females
in Graham Land series
of ovaries.*

*No. of
c. lutea.*

*No. of
females.*

*No. of
c. lutea.*

CASE B

*No. of
females.*

*No. of
c. lutea*

9
14
9
9
5
2
1
1
1
1
1
—
53 females.

1
2
3
4
5
6
7
8
9
10
14

100
95
90
85
80
70
60
40
10
1
—
631 females.

1
2
3
4
5
6
7
8
9
10

100
95
90
85
261
—
631 females.

1
2
3
4
5

CASE C

*No. of
females.*

*No. of
c. lutea.*

100
95
90
185
101
60
—
631 females.

1
2
3
4
5
6

When these frequency distributions of corpora lutea are set out graphically (fig. 19) it is very clear that unless the corpora persist throughout life, there must be some most 'fashionable' number, even in the case when the presumptive life of the corpus is somewhat variable in length. In the same diagram are shown the actual numbers of individuals possessing each number of corpora lutea as found by examination of 53 pairs of Weddell ovaries from Graham Land. In this series it is reasonably certain that the relative fewness of females possessing a single corpus is

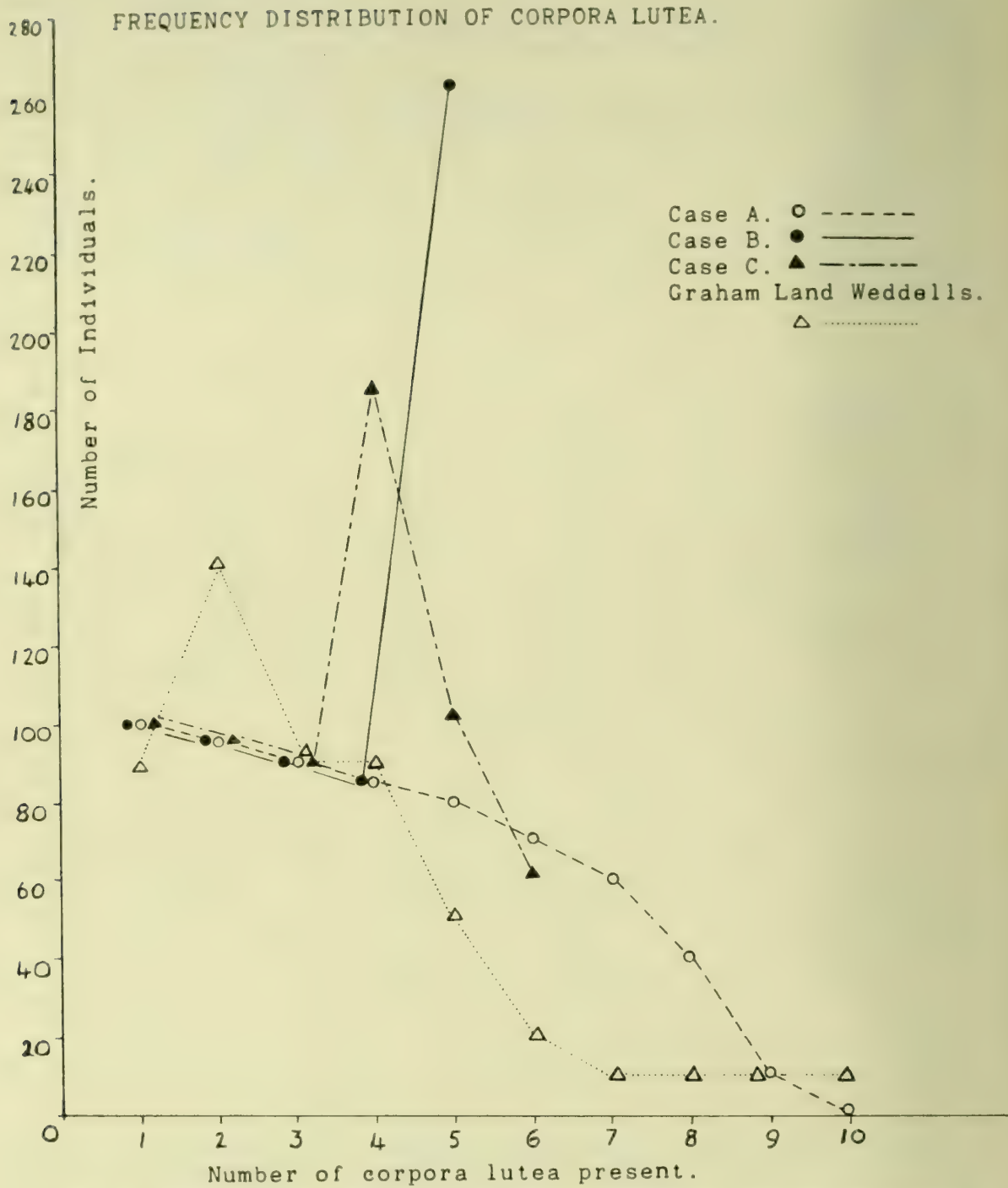


FIG. 19.—Diagram to show what would be the frequency distribution of corpora lutea in the ovaries of a hypothetical population of seals on the basis of each of three alternative assumptions. The actual frequency distribution in the Graham Land series of Weddell ovaries is also included (actual numbers $\times 10$).

due to differences in lying out habits, resulting in faulty sampling of the population. (This point is explained later at greater length, p. 67-8.) It is clear that the Graham Land curve far more closely resembles hypothetical curve A rather than B or C. As in case A, each higher number of corpora lutea present in the ovaries is represented by a smaller number of animals. Therefore, it is reasonable to conclude that in the Weddell seal the corpora lutea persist throughout life (which happens for a variety of reasons to be rather short). This is not to say that some corpora lutea may not be rather small and difficult to recognize as such in the older animals, for almost certainly they do continue to diminish in size with the progress of time. It so happens in the species that normally the individual dies before the first-formed corpora lutea have become unrecognizable.

Thus all the ovulations in the life of the individual Weddell seal are believed to be permanently recorded in the ovaries by their representative corpora. Since there is every probability that the normal Weddell female ovulates but once each year, and that successfully, it is clear that examination of the ovaries gives a direct determination of the number of pregnancies undergone by the individual female. Slight allowance may perhaps be made for the 'missed pregnancies', which are found (see p. 66) to constitute about 16 per cent of the adult female population at any one time, but it is clear that the ovaries can give a very fair indication of the probable age of the individual female Weddell seal. There will doubtless be certain exceptions and anomalous individuals, but taken as a whole we are here provided with a fair method of determining female ages. The probable age of the individual seal is given by adding the 2 years of her pre-adult life to the number of corpora lutea that can be counted in her ovaries.

The evidence in certain directions, owing to lack of enough material, cannot provide absolute proof of this conclusion, but it points strongly towards it; and there is nothing in the data that is incompatible with it.

(b) '*Missed*' *Pregnancies*

A small number of the female Weddells killed were found not to be pregnant during the period when most of the females were in that condition. This fact is important because of the previous conclusion that it is possible to judge the age of the individual from the number of old corpora lutea in the ovaries. Estimates have therefore been made of the proportion of adult females that were 'missing' pregnancy. In making this estimate only those seals killed between February and August inclusive can fairly be included, and this much reduces the number of animals on which the conclusions must be based. During these months the pregnant and non-pregnant seals, if lying out, were equally likely to be killed. September seals are excluded because of the pupping season with consequent possible mistakes over seals that had perhaps pupped at a rather early date and lost their pups subsequently. January seals are excluded because at that time it was not always quite possible by looking at the uterus to determine rapidly whether or not the seal really was pregnant. Using then the seals killed from February to August inclusive, the following results are obtained

No. 1 (e)

		<i>Pregnant</i>	<i>Non-Pregnant</i>
Females under	80 in.	0.... 0 per cent	11
Females	80-84 in.	1.... 10 per cent	10
Females	85-89 in.	1.... 25 per cent	3
Females	90-94 in.	11.... 84½ per cent	2
Females	95-99 in.	6.... 75 per cent	2
Females	100-104 in.	3.... 75 per cent	1
Females over	104 in.	3.... 100 per cent	0

The 85-89 in. group is by chance very small: if the January and September seals be included, the figures for this group are 'Pregnant 6' and 'Not pregnant 7', with the chance that some of the January seals were really pregnant but not noted as such. It is clear that the length group 85-89 in. represents the usual size at which the Weddell seals attain sexual maturity. Of females 90 in. and over taken together the 'missed' pregnancies amount to 16 per cent. It seems probable from the figures that these really are 'missed' pregnancies and not due to seals that have grown abnormally large before attaining sexual maturity.

Whether the seals on which this estimate of 16 per cent of 'missed' pregnancies is based can be taken as a fair sample of the female Weddell population is somewhat open to doubt, however. It might be supposed that the pregnant female, having a rapidly growing foetus to nourish, and feeling the biological necessity of acquiring an ample thickness of blubber to stand the strain of lactation, would spend proportionately more time feeding and less in lying out. Killing of the seals could only take place when they were lying out; hence there is a chance that an undue proportion of the non-pregnant population was taken. This error is quite possible, but in the absence of much more extensive figures it is not possible to check the point. Therefore it may be tentatively concluded that of the sexually mature female Weddells about 16 per cent fail to become pregnant each year.

The result of a missed pregnancy so far as it is reflected by the corpora lutea is more doubtful. There are various possibilities.

(a) The seal may actually have become pregnant at the normal time, and later, by mischance or disease, the foetus may have been lost. Ovaries 1454 are from a 95-in. seal that was perhaps in this condition. In this animal there were fibroids in the uterus and no foetus was present on 29/2/36. At this time of year the normal foetus is about 12 cm. long. There was an apparently functional corpus luteum, also a 10-mm. follicle in each ovary. The ovary with the functional-type corpus contained one old one, while the opposite ovary contained three others. At the time of killing it was not possible to make a detailed examination of the whole of the uterine lining, so that it cannot be said with certainty whether or not the uterus had recently contained a foetus. It is not therefore known whether the large corpus seen represented a sometime functional one of pregnancy recently terminated and that had not yet had time to regress, or whether it represented a newer and unsuccessful ovulation. In the latter case a count of all the corpora lutea present might give a number one greater than the age of the animal would normally warrant.

(b) Any seal missing pregnancy may be doing so because, though ovulating, she failed to be impregnated. Presumably the corpus luteum of unsuccessful

ovulation would leave its permanent record just as does the corpus of pregnancy. In this case the number of corpora will be the same as if there had been a successful pregnancy. On the other hand the material available is not extensive enough to give any absolute proof of whether, after unsuccessful ovulation, further ovulations can or cannot occur. That is to say, the complete proof that the Weddell seal is monoestrous rather than polyoestrous (and normally successful at the first ovulation) is lacking, but there is a strong presumption that further ovulations do not occur. Ovaries 1128, dated 11/4/35 (from a non-pregnant seal), may be significant in this direction. Here there are no old corpora lutea present in either ovary, but in one there is a rather irregular partly regressed corpus 15 mm. across. In addition there are a 10 mm. and a 4 mm. follicle in the same ovary as this corpus, and two 6-mm. follicles in the other. It is suggested that this irregular corpus luteum represents the result of an unsuccessful ovulation. It is now clearly regressing, but if it was produced as the result of an ovulation at the normal time (in December) its life had been rather longer than might perhaps have been expected. Whether at a rather later date the 10-mm. follicle would develop still further and actually ovulate it is impossible to say. The general fewness of old corpora lutea in Weddell ovaries on the whole suggests that further ovulation is unlikely, though the single case of a seal with 14 old corpora (while no other seal had more than 10) perhaps indicates that occasionally it does take place.

(c) The third possibility is that the seal missing pregnancy may be doing so simply because she failed to ovulate. In this case the number of corpora in the ovaries will be one less than her age would normally warrant.

The result of this summary of the possible effects of 'missed' pregnancies on the accuracy of interpretation of the counts of corpora lutea is that no great error is likely to be involved on their account, so that, until further evidence is available, they may be neglected.

(c) *Frequency Distribution of Corpora lutea*

The observed frequency distribution of the numbers of corpora lutea in the ovaries has already been used as evidence for the permanence of these bodies, but there is one further point that needs some explanation. In any wild population of animals that is relatively stable, or at least is not fluctuating greatly, the number of individuals in any one age group should be greater than the number in any older group. Taking old corpora lutea as measures of years, this numerical age distribution was observed with the exception of the first group of all (see fig. 19). This first group of all, instead of being larger than any succeeding one, was actually somewhat less than the next succeeding, and of the same size as the two following that. This anomaly is by no means enough to embarrass the argument used in proving the permanence of the corpora lutea, but none the less requires some further consideration. The following, in the view of the writer, is the most probable explanation.

The Weddell population can only be sampled by killing the animals when they have left the water. Therefore if there be any variations in lying out habits between seals of different ages, these differences will be reflected in the numbers of the different age groups that are taken. Thus (as pointed out elsewhere) the seals examined by

no means necessarily represent a true sample of the population as a whole. In the present instance it is suggested that the class of female Weddells containing a single corpus luteum in their ovaries (i.e. seals now pregnant, or just pupped for the first time) were not taken in quite their true proportion relative to the population as a

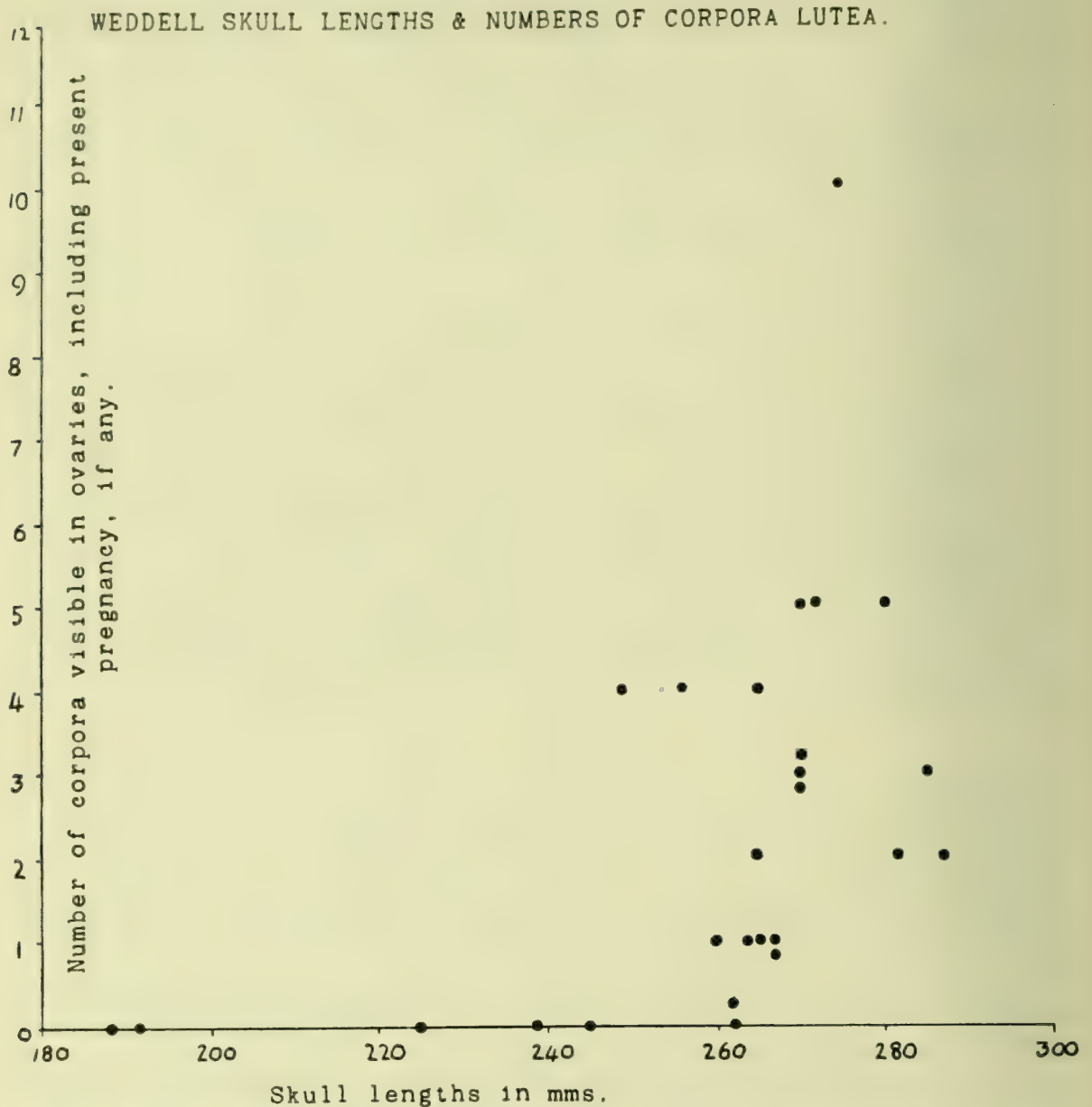


FIG. 20.—Diagram to show the relation between the skull length and the numbers of corpora lutea in the Graham Land series.

whole. Before they become pregnant for the first time the female Weddell seals certainly lie out in very small numbers, and are indeed rarely seen. At the pupping season the females pupping for the first time necessarily behave as do their elders. But during their first pregnancy it may well be that this group of young seals retains

to some degree the juvenile habit of remaining almost always in the water. Hence this youngest group is not represented in the figures in proportion to its true strength.

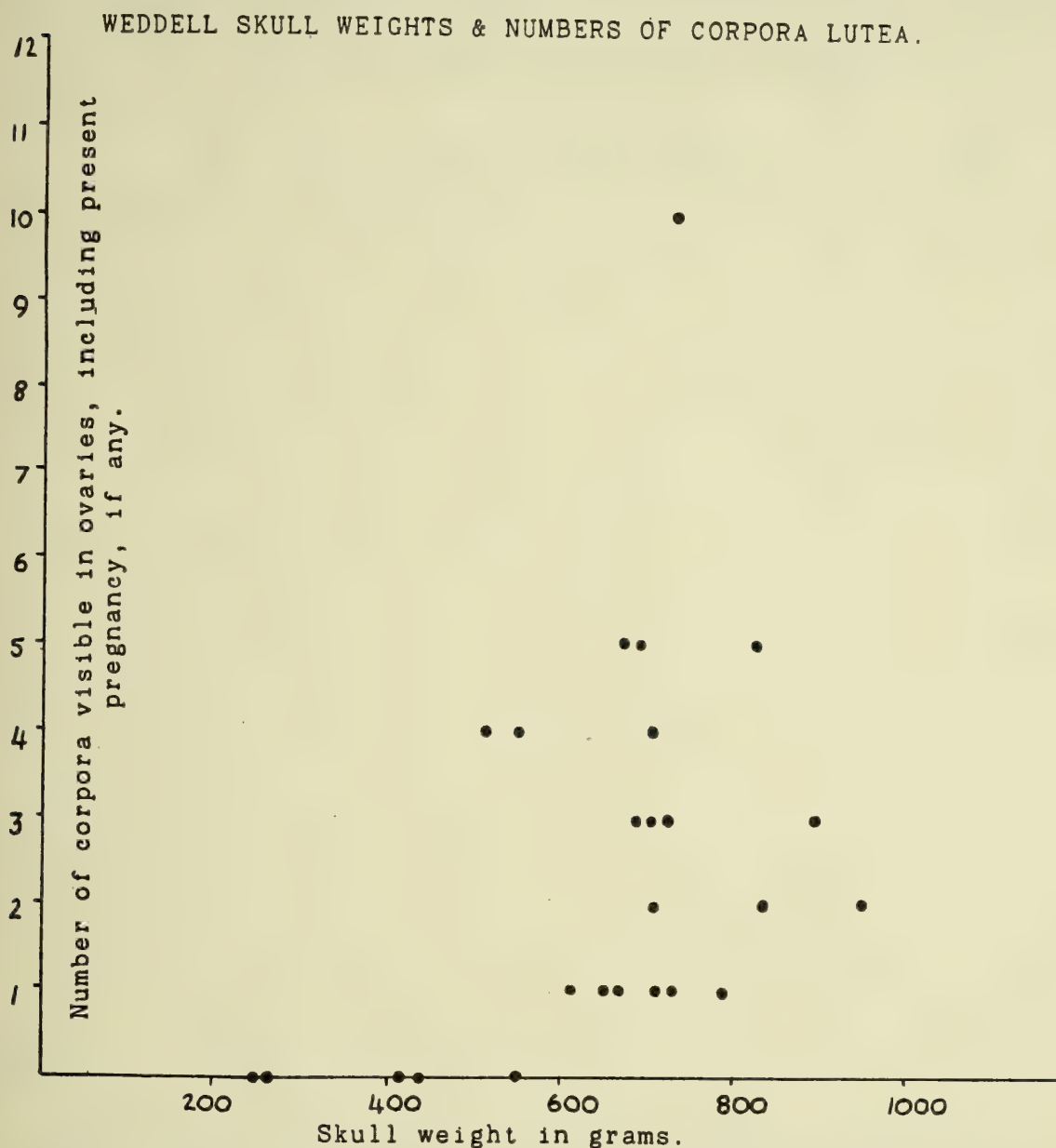


FIG. 21.—Diagram to show the relation between the skull weight and the numbers of corpora lutea in the Graham Land series of Weddells.

CORRELATIONS AND AGE DETERMINATION

It now remains to examine the correlation, if any, between the various skull dimensions and proportions and the closure of the sutures, with the number of persisting corpora lutea in the ovaries. As already shown, there is too much variation in growth for the body length of the Weddell seal to be used as a precise criterion of

age beyond the first 2 years, and its accuracy is doubtful even so far as that. This variation in growth may include both actual differences in growth rates between individuals, and individual cessation of growth at different sizes. Despite this individual variation, it has been shown in the previous section that there is a good correlation between the number of corpora lutea and body length, since whatever the variation in length, its increase must always be a function of time.

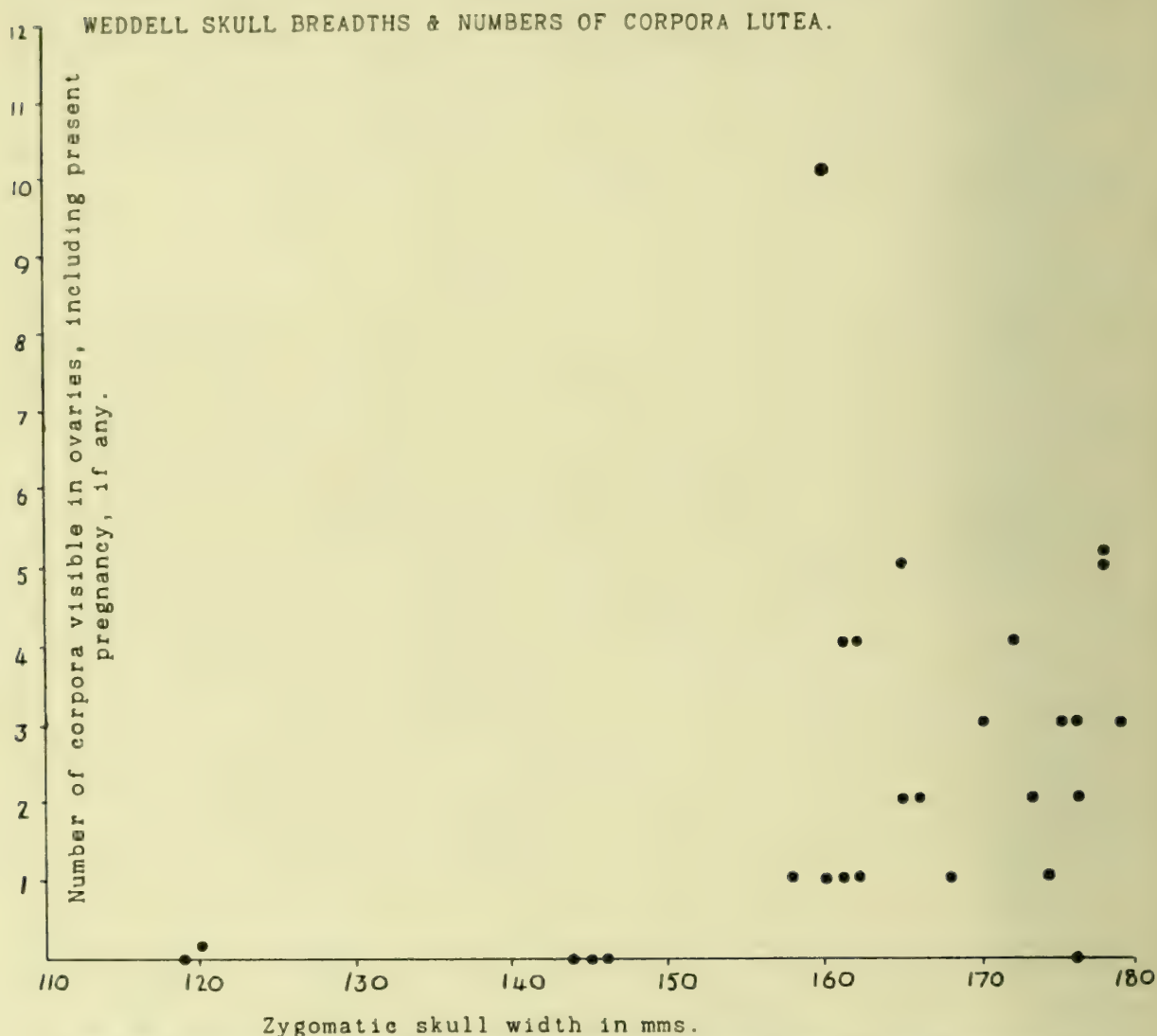


FIG. 22.—Diagram to show the relation between the skull breadth and the numbers of corpora lutea in the Graham Land series of Weddells.

When these numbers of corpora (*ex hypothesi* measures of age) are plotted against either skull length, skull weight, zygomatic width or proportionate width, it is found that the individual variations are almost great enough to mask completely the underlying tendency for parallel increase (figs. 20–23). From a comparison of the figures it seems probable that the absolute zygomatic width is more nearly a direct measure of age than any of the other three factors here enumerated.

The relationship is shown diagrammatically (fig. 24) between the closure of certain sutures in a series of 25 female Weddells in which the skulls, the body lengths and the numbers of corpora, and the amount of wear of the ice-sawing teeth are all known. When the skulls are placed in order of numbers of corpora lutea, the closure of the sutures in the series is more regular than when the skulls are placed in order of

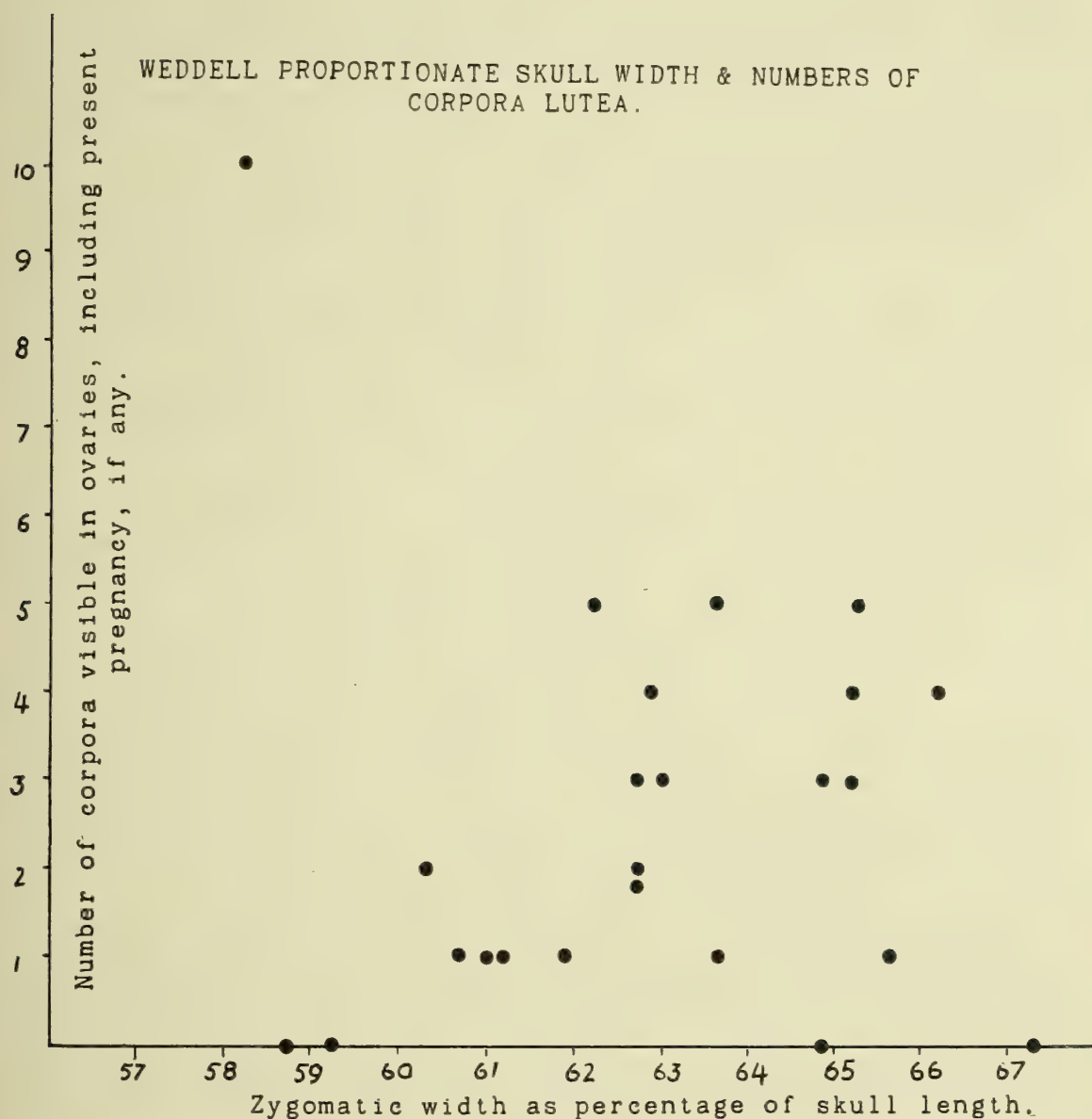


FIG. 23.—Diagram to show the relation between the proportionate skull breadth (i.e. zygomatic width as a percentage of skull length) and the numbers of corpora lutea in the Graham Land series of Weddells.

length. As already pointed out, skull lengths and corporal numbers are obviously to some degree related, but there is now the suggestion that closure of certain of the sutures is more a function of age than of size of the skull. Even so, the individual variations are great, and the amount of closure of various sutures in the same animal seem sometimes to bear little relation to one another.

A series of 19 skulls of female Weddells all killed in January (but for No. 131 in December) has been selected for further consideration. The ovaries of all these 19 seals having been examined and an *ex hypothesi* age given to the animals, it is possible to compare the grouping by ovarian ages with whatever grouping might be possible by means of body and skull dimensions in conjunction with one another (Table p. 74). Since seals killed in one month (i.e. January) alone are considered, the animals must be roughly 4, 16, 28, 40, etc., months old, the 28-month individuals being just pregnant for the first time.

When the dimensions of these 19 skulls are set out graphically, likewise their body lengths (fig. 26, black spots), it is apparent that, apart from three small individuals no certain grouping is possible on this basis alone unless one or other dimension be assumed to be of much greater significance than any other. The three small seals were 173, 188, and 193 cm. in length. Consideration of the curves of growth in body and skull length, and the appearance of the skulls themselves, shows that there is little doubt that the 173-cm. seal was 4 months old, the 188- and the 193-cm. seals being 16 months old. Beyond this point individual variations in growth have evidently been so great as to mask any visible tendency to fall into year groups based on dimensions alone. If the amount of data were vastly greater, conceivably it might be possible to detect a real grouping despite the variations. In the diagram (fig. 26) the numbers of corpora lutea (assumed to give a nearly absolute measure of age) have also been inserted for convenience and comparison.

The conclusion already reached that after the first two years of life, the year groups of the Weddell seal cannot be distinguished (except by examination of the ovaries) is thus further strengthened. That the evidence as to probable individual ages obtained from the ovaries in a general way agrees with the dimensional data, has already been shown. The ovarian data may now be compared with the general characters of the skulls rather than their dimensions alone. To this end the series already used of 19 skulls taken from seals killed in the same month is again considered, here in relation to numbers of corpora lutea.

Of the four seals in the series of 19 that have a corporal number of 0, one (No. 99) is markedly dissimilar from the other three, being very much larger, and will be considered shortly. The remaining three skulls (Nos. 137, 140, and 113) are from seals much smaller in body length than any others in the series, and their zygomatic widths likewise are very much smaller. The lengths of these three skulls, especially of No. 113) more nearly approach that of the larger seals of the series. One of the three (137) is much smaller in skull length and body length than the other two, and differs from them also in the state of closure of the sutures and the somewhat smaller size of the canines. No. 137 is in fact juvenile compared with Nos. 140 and 113. The sutures of the cranium proper are the most significant in the present consideration. All three have the basisphenoid-basioccipital and parieto-frontal sutures completely open, but in No. 137 the parieto-squamosal, inter-parietal and inter-frontal sutures are all

Skull No.	Skull length in mm.	Body length in in.	Parieto-frontal suture.	Basioccipito-basisphenoid suture	Anterior. ← Inter-premaxillary and inter-maxillary sutures.	Anterior. ← Interpalatine suture.	Maxillo-palatine suture.	Amount of wear of upper canines. 0 = no wear. 3 = most wear.	Number of corpora lutea.
137	225	68	-----	-----	-----	-----	-----	0	0
140	239	76	-----	-----	-----	-----	-----	0	0
113	245	74	-----	-----	-----	-----	-----	0	0
99	260	96	-----	-----	-----	-----	-----	1	0
32	253	90	-----	-----	-----	-----	-----	1	1
95	255	87	-----	-----	-----	-----	-----	1	1
138	255	90	-----	-----	-----	-----	-----	0	1
102	262	88	-----	-----	-----	-----	-----	1	1
62	265	97	-----	-----	-----	-----	-----	3	1
44	265	95	-----	-----	-----	-----	-----	3	1
98	—	92	-----	?	-----	-----	-----	2	2
104	260	99	-----	-----	-----	-----	-----	1	2
107	272	97	-----	-----	-----	-----	-----	3	2
100	281	102	-----	-----	-----	-----	-----	2	2
141	261	90	-----	-----	-----	-----	-----	2	3
131	263	90	-----	-----	-----	-----	-----	3	3
112	265	98	-----	-----	-----	-----	-----	1	3
105	279	99	-----	-----	-----	-----	-----	2	3
135	246	86	-----	-----	-----	-----	-----	2	4
97	249	89	-----	-----	-----	-----	-----	2	4
136	263	98	-----	-----	-----	-----	-----	3	4
101	261	100	-----	-----	-----	-----	-----	2	5
30	263	104	-----	-----	-----	-----	-----	3	5
65	278	110	-----	-----	-----	-----	-----	3	5
35	269	100	-----	-----	-----	-----	-----	3	10

Suture open -----; Suture closed ———.

FIG. 24.—Table to show the closure of certain important sutures in the skulls of a series of female Weddell seals from Graham Land, in which the body length and the number of corpora lutea in the ovaries are known. The skulls are arranged in groups by numbers of corpora lutea, and by skull length within each such groups.

<i>Skull No.</i>	<i>Body length in cm.</i>	<i>Skull length in mm.</i>	<i>Skull width in mm.</i>	<i>'Corporal' number including present pregnancy if any.</i>	<i>Probable age in months.</i>
137	173	225	146	0	4
140	193	239	144	0	16
113	188	245	145	0	16
99	244	262	176	0	28
95	220	264	161	1	28
102	223	267	162	1	28
138	228	262	160	1	28
100	259	287	173	2	40
104	251	265	166	2	40
98	234	—	165	2	40
107	246	281	176	2	40
112	249	270	170	3	40 +
141	228	270	175	3	40 +
131	228	270	176	3	40 +
105	251	285	179	3	40 +
135	217	249	162	4	40 +
97	225	256	161	4	40 +
136	249	265	172	4	40 +
101	254	272	178	5	40 +

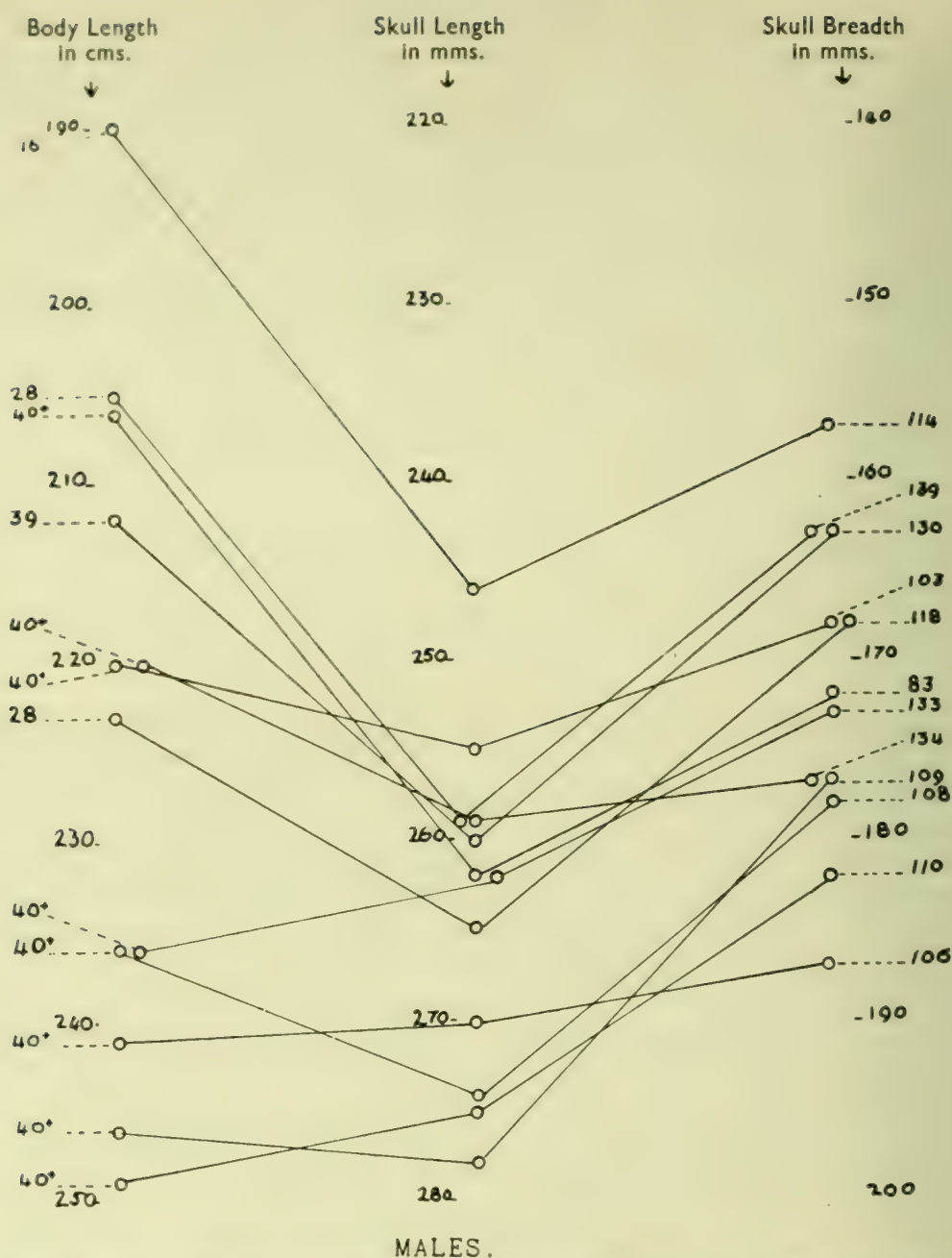
Table to show the characters of a series of 19 female Weddell seals selected as having all been killed at about the same time of year (i.e., December or January), and therefore being of the same age or separated by an exact number of years.

distinct as well, while in Nos. 140 and 113 these latter sutures have all but disappeared. There can, in fact, be little doubt that whereas No. 137 is from a 4-month seal, Nos. 140 and 113 are from animals 1 year older (i.e., 16 months).

Now comes the question of No. 99, which was similar to Nos. 137, 140, and 113, in the complete lack of corpora lutea in the ovaries, but is otherwise very different in being greatly bigger and coming from an animal 96 in. in length. Whereas, too, the ovaries of the three smaller seals were completely infantile, those of No. 99 were much bigger and contained a follicle 8 mm. across. No. 99 cannot possibly be classed with the 4- and 16-month individuals described, but is very similar to Nos. 95, 102, and 138, whose corporal number is 1, and which are evidently 28-month-old seals now just pregnant for the first time. Why No. 99 failed to become pregnant when they did is of course unknown; the chance of the 8 mm. follicle ripening and the animal becoming pregnant a few weeks later is to be ruled out, since were that the case there would be created an irregularity of pupping that is never found. Presumably, however, a few seals may always mature a little slowly and fail to become pregnant at exactly the normal time, or by some peculiar mischance may fail to be impregnated. Some such reasoning must account for No. 99, which in general characters tallies with skulls Nos. 95, 102, and 138, here believed to be 28 months old.

These four skulls may now be treated together as representing the third-year group of the present series. As the diagram shows, there are considerable variations in the size of these four skulls and the lengths of the animals from which they came, and henceforth the value of size as a diagnostic of age is very slight or non-existent. The four skulls are obviously relatively 'young', for in all of them the basisphenoid-basioccipital suture is still open, except possibly for a small amount of coalescence medially. In all of them the parieto-frontal suture is still open for roughly half of its length on either side, the closure starting dorsally and extending ventrally. In none of the four is there obliteration of the sutures of the palate. Likewise all four skulls show relative youthfulness in the condition of the teeth, which are practically perfect, with the points of the canines and incisors only slightly rounded by ice-sawing.

All the remaining 12 of the 19 selected skulls taken at the same time of year show definite signs of greater maturity. The ovarian evidence alone for these 12 skulls suggests the following grouping: 4 at 40 months, 4 at 52 months, 3 at 64 months, and 1 at 76 months. The ovaries thus suggest that the oldest skull in the series is from a seal 6 years and 4 months old, with corporal number 5, being now just pregnant for the fifth time. The 4-month and the 16-month skulls, as we have seen, were separable from the others on the score of dimensions and appearance, quite apart from the ovarian evidence. The 28-month skulls also are separable from those both younger and older by appearance (i.e. closure of sutures, etc.), but not on that of size from those older. The 40-month and over skulls are likewise separable from all those younger by appearance; but the division of these older skulls into actual groups by any means other than ovarian examination is very doubtful. In all of them the basisphenoid-basioccipital suture is almost completely closed, though the extreme lateral extremities often remain open when the medial portion has long disappeared completely. The sutures of the palate of these 40-month and over skulls are in various stages of disappearance, this taking place rather



FIGS. 25 and 26.—Composite diagrams to illustrate the dimensional basis of the year groups of male and female Weddell seals in the Graham Land series. Only those seals are included that were killed in either December or January, so that all must have been of the same age, or separated by a precise number of years. Lines join the reference marks belonging to each individual. To facilitate reference the serial number of each skull is inserted to the right, and the final estimate of its age in months to the left. This estimate of age is based on the degree of closure of skull sutures in addition to the dimensional and ovarian data shown in the present diagram. The symbols —, ·, ··, ···, etc., indicate the presence in the ovaries of the individual seal of 0, 1, 2, or 3, etc., corpora lutea, including that of the present pregnancy if any. Where unmarked in this way there is an element of doubt (one case only). The use of a broken line indicates that the ovaries were not examined. In such cases the symbols * and — indicate (in those cases where the ovaries were not preserved) that the animal is known to have been 'not pregnant' or 'pregnant' respectively. In fig. 26 full spots indicate members of the group of 19 females that receive special consideration in the text, while open circles represent those females for which the data are incomplete.

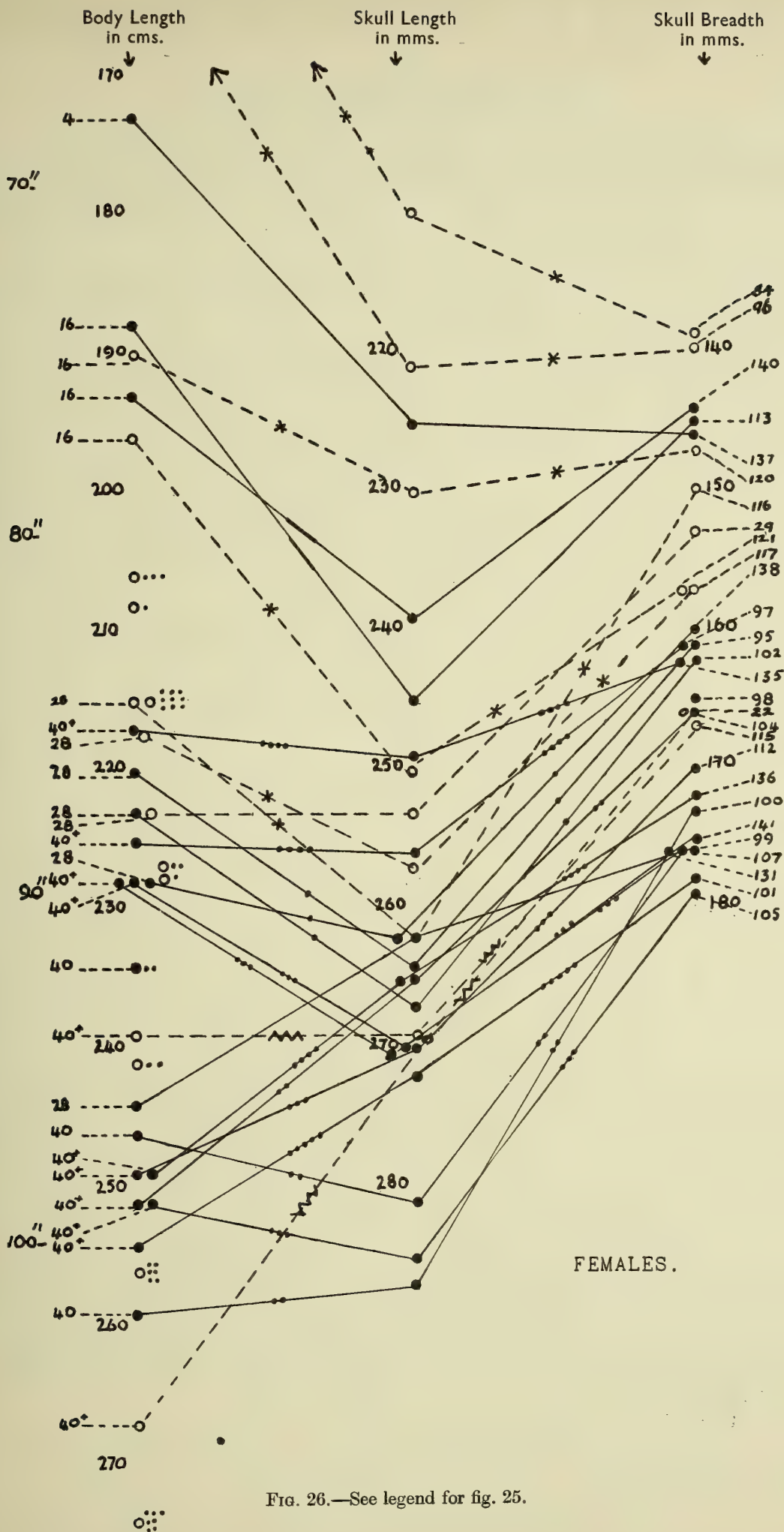


FIG. 26.—See legend for fig. 25.

irregularly, but in general beginning anteriorly with the inter-premaxillary and gradually extending back along the inter-maxillary, but in none of them have the inter-palatine and palato-maxillary sutures disappeared. The parieto-frontal sutures have more or less disappeared, though there are great variations in this (e.g. see description of skull No. 101 below).

The teeth of this group of 40-month and over skulls are all more worn than, or at least as much worn as, those of the 28-month group. In several cases the canines and incisors, especially those of the upper jaw, are much rounded at the tips from ice-sawing. Although in all cases the cheek teeth are still in good condition, several of the animals have suffered breakages of the canines and incisors, especially in the upper jaw. Quite apart from wear at the tips and these breakages, there are also cases of wear between the teeth, the parts affected mostly being the adjacent anterior surfaces of the upper canines and posterior surfaces of the lower canines (as is common in carnivores).

Of these older skulls, three possess points to which special reference must be made. No. 135, coming from an 86-in. animal, is the smallest of all the skulls of mature seals. The ovaries suggest the age as 64 months being now just pregnant for the fourth time. Despite the small size the skull is, by comparison, very completely ossified. The basisphenoid-basioccipital suture is completely invisible, as is the parieto-frontal except for about 1 cm. ventrally on either hand. The inter-premaxillary and maxillary sutures are quite closed and the inter-maxillary is beginning to be so. The teeth and their sockets are on the whole in good condition; the ice-sawing teeth are somewhat worn and the first pair of lower incisors, extremely small in this individual, are broken. The fifth upper cheek tooth on the right side has never completely erupted, its tip being visible but not protruding.

Female skull No. 101 is peculiar. As can be seen in the diagram (fig. 26), it is clearly the skull of an old seal. Proportionately it is a very broad skull, and in general it is as well 'developed' as almost any skull in the whole collection, the mandible being particularly massive for a female. It is in the condition of the parieto-frontal suture that No. 101 is chiefly remarkable. This suture even in the 28-month seals is normally already obliterated through at least half its length. In No. 101 this suture is completely open throughout. The other sutures of No. 101 are scarcely visible, as would be expected in an old animal. The basisphenoid-basioccipital is obliterated in the centre, but, as is often the case, is still extant laterally. The sutures of the anterior part of the palate have almost completely disappeared, and even the inter-premaxillary and maxillary sutures in anterior or dorsal aspect are vanishing. The open condition of the parieto-frontal suture is but one more example of the extreme variability that is found in this species of seal.

Now that this series of skulls, taken from seals killed at the same time of year, has been examined with the aid of 'ovarian' ages, the other skulls of Weddells can be for the most part fitted into the series. It is clear that the closure of the sutures is a far more reliable guide to age than is any one dimension or combination of dimensions. It seems that the skulls can be separated with reasonable certainty into the first three year-groups, for example, 4-month, 16-month, and 28-month seals are distinguishable from one another and from all older (plates V, VI). But the '40-plus'-month skulls, though separable from all younger, are not distinguishable directly

among themselves. If, however, the '40-plus'-month skulls are grouped simply according to known 'ovarian' ages, there is a general agreement between greater age and skull appearance, for example, wear of the ice-sawing teeth and closure of palate sutures.

This series of female skulls, whose ages have now been deduced with reasonable certainty, can be used as a basis for determining the age of the male skulls. Direct comparison of the two sex series of skulls, and consideration of their dimensions, bring to light no feature that would suggest that the male skull in growth or development differs in any important particular from the female. The male skulls, like the female, seem to be divisible into year-groups with fair certainty in the early stages, but later all distinctions disappear. There seems, in the Graham Land series of skulls, to be a tendency for a greater proportion of the males to have the palate sutures in an advanced state of fusion. Whether this represents a senile feature appearing at an earlier age than in the female, or the attainment of a greater age by a larger proportion of the male population, is not known.

Now that it has been possible to place the female skulls (and the males too by direct comparison) in age series up to the age of about 40 months on a combined basis of osteological features and ovarian examination, the various skull dimensions may be compared direct with the assumed ages (figs. 27, 28, 29). In the diagram the '40-plus'-month skulls, not being further separable, are grouped together. The 'ovarian' age is indicated where known in the case of the female skulls. 'Age in months' is equal roughly to '26 plus 12 times the "ovarian" age'. Thus it becomes possible to construct true growth curves for the various characters (i.e. body length, skull length and weight, etc.) up to the age of 40 months. From these it is clear that a character such as skull length increases at a much more regular rate than, say, skull weight. At the same time individual variations in all characters are manifested at an early age, so that age estimations of individual seals, from measurements only, must always be accepted with caution.

THE COMPOSITION OF THE WEDDELL SEAL POPULATION

Consideration has now shown that though it is not possible to determine the age of individual Weddell seals with any sureness except in the early stages (at best up to 40 months of age), from their body sizes, skull characters or dimensions, it is possible to do so in the case of the older females with a fair degree of probability from an examination of the number of corpora lutea in their ovaries. In a series of 53 pairs of ovaries from breeding females, the age distribution judged in this way was as follows:

Number of corpora lutea, including																			
present pregnancy, if any	1	2	3	4	5	6	7	8	9	10	..	14					
Age of the individual seals at the next																			
pupping time in years	3	4	5	6	7	8	9	10	11	12	..	16					
Number of individuals at each of these																			
ages	9	14	9	9	5	2	1	1	1	1	..	1					

It has already been pointed out how this frequency distribution is itself confirmatory evidence for the truth of the method of age determination used. The series is unfortunately not as extensive as one would wish, but certain conclusions may

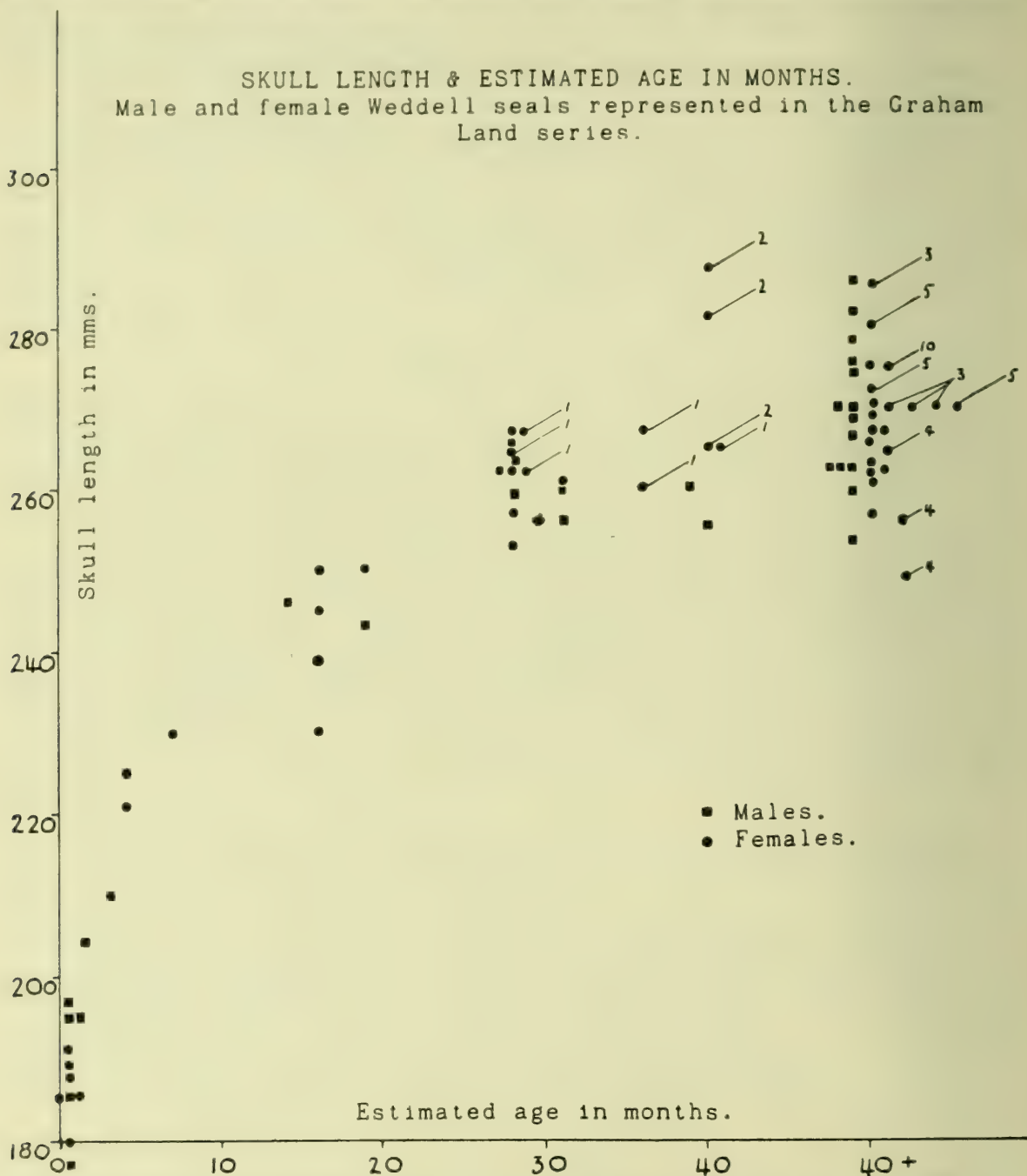


FIG. 27.—Diagram to show the relation between the skull length and the estimated age in months of the male and female Weddell skulls in the Graham Land series. Where known, the number of corpora lutea in the ovaries of the animal from which the skull came is appended.

be drawn. The most obvious feature is the shortness of life of the average female Weddell seal, few apparently surviving to pup more than six times.

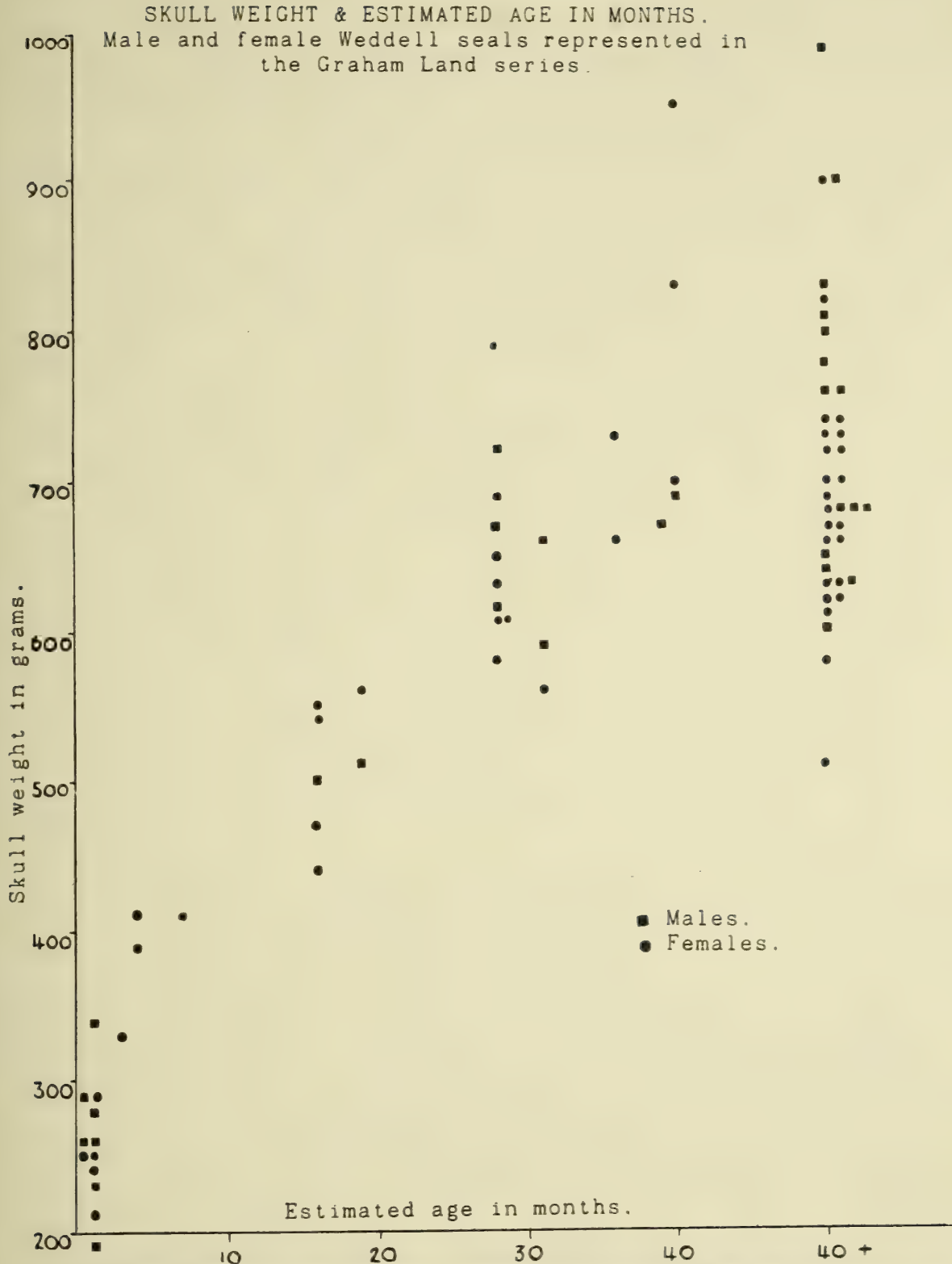


FIG. 28.—Diagram to show the relation between the weight and the estimated age in months of male and female Weddell skulls in the Graham Land series.

No. 1 (*f*)

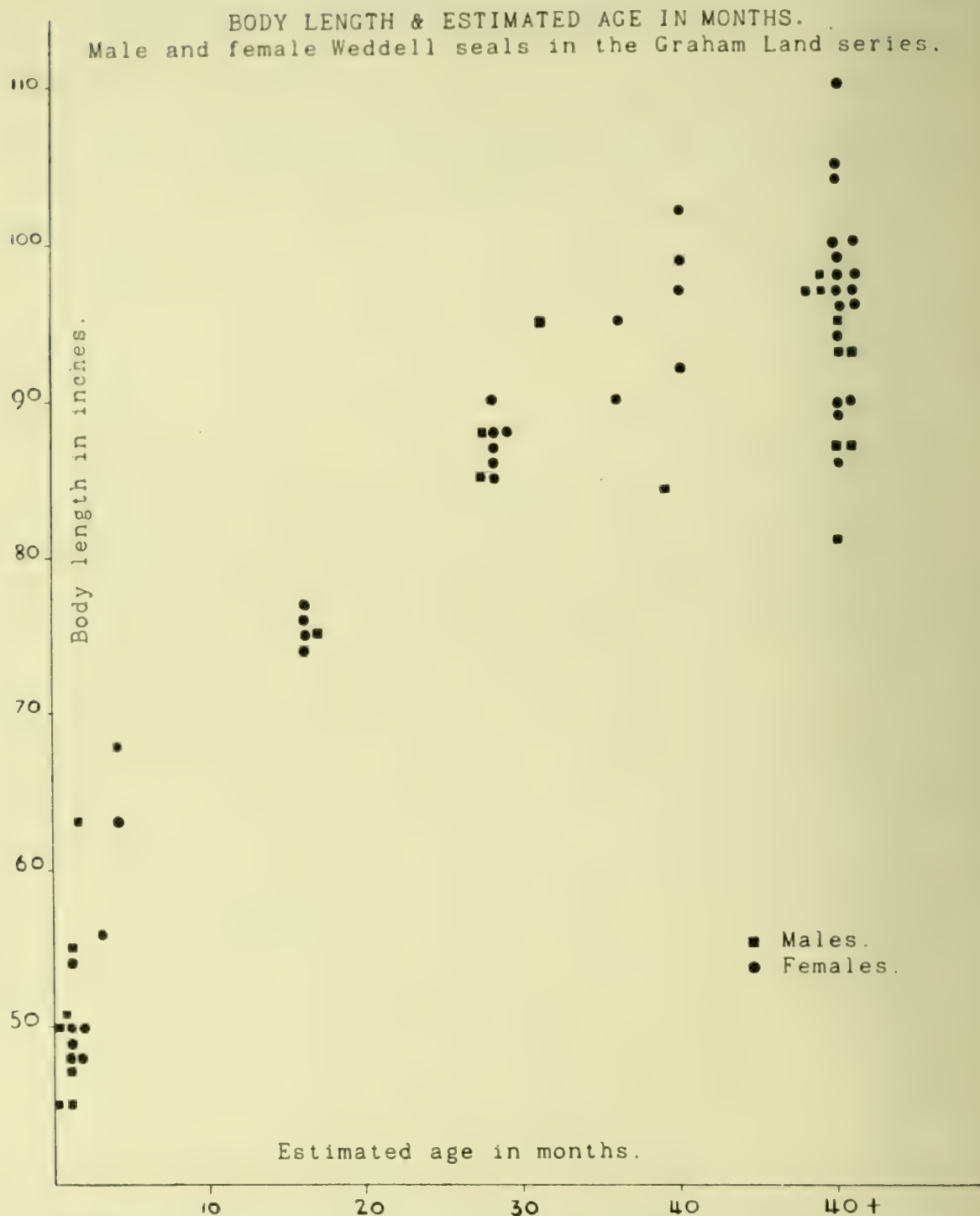


FIG. 29.—Diagram to show the relation between the body length and the estimated age in months of male and female Weddells in the Graham Land skull series.

It became quite clear early in the field observations that the youthful seals were taken in far less proportion than they must exist in the population as a whole. Once the young seals take to the water, very little is seen of them until they are pregnant for the first time (i.e. during their third year), and even then it is doubtful whether they are taken in their true proportion. In early life the animals are growing most rapidly, and so they must presumably spend a greater proportion of their time feeding. Hence one might perhaps predict that they would be found lying out less frequently. Since the animals can be killed only when they are lying out, the frequency with which the various age groups are represented is clearly determined by their habits in this respect. That body length is a fairly direct guide to age for the first year, or 2 years, has already been shown. The diagrams of body growth at once demonstrate the paucity of younger seals that put themselves in a position to be killed.

When, as with the Weddell seal under consideration, there is no reason to believe that a population of animals is undergoing violent fluctuations, it must happen that the number of individuals in any one age group is greater than the number in the next older age group. In the present case, represented by the age distribution figures above (based on ovarian evidence), we have no knowledge of the sizes of the immature year groups relative to those of the adult seals except that these earlier groups must be larger. How much larger cannot be known directly until some other method of taking a sample of the population is devised than killing the seals when lying out on the ice or beaches, or alternatively some reliable estimate can be made of the mortality in the early years. All that is known at present is that, in a rookery studied by Lindsey (1937), the mortality was between 10 per cent and 20 per cent, among the pups in the first 7 or 8 weeks of life before they had finally separated from their mothers. During the next short phase, when the young seals are making the transition to the adult diet, one might expect the death rate among them to continue high. Beyond that nothing is known of the death rate until the female seals are sexually mature.

As to the male seals, in these various respects, nothing definite is known in the absence of a method of determining their individual ages beyond about 40 months, but there is nothing to suggest that their age distribution is markedly different from that of the females. Of the mature female Weddells, after having pupped for the first time, it is believed that those killed and here considered, give a true picture of the state of the population as a whole. The average age (at the next pupping time) of this sample of adult female seals (whose ovaries have been examined) is 5.3 years.¹ This means that when the present pregnancy has terminated, the 'average' female will have had 3.3 pups, since each seal pups on completing the third and each succeeding year of her life. The 53 seals on which the figures are based are a small representative fraction of the whole female Weddell population, and the actual breeding stock at any time will be some multiple of these figures, i.e. $(9 +)N$ 3-year-old seals, $14N$ 4-year-old seals, $9N$ 5-year-old, and so on. Assuming that every adult seal pups each year (actually about 16 per cent 'miss' pregnancy each year), the annual crop of pups is $53N$ in the whole population. On consideration it is clear that under existing

¹ For the present purposes the 3-year-old seals being presumed equal in numbers to the 4-year-olds, though actually they must be rather more numerous than that.

mortality conditions, and assuming the population to be stable, a total of 53N is also the number of pups that should be born in the total life histories of all seals born in the same year. But at any given date under the existing mortality conditions there are $(9 +)N$ female seals breeding for the first time. That is to say, in the total life histories of these $(9 +)N$ seals, there will be produced by them 53N pups. Therefore the average number of pups born to each female that reaches sexual maturity will be about five if the population is to remain constant. The sex ratio at birth is probably not very far from equality, though there seems to be a tendency for males to preponderate.

For the population to remain constant each female must be survived by one daughter reaching sexual maturity. It therefore seems probable that under the existing mortality rates about 50 per cent of the female seals born attain sexual maturity.¹ Thereafter the mortality rate among the female seals will be such as to allow of the production of age classes as shown in the table of figures for female ages (p. 79).

THE CRABEATER SEAL

Lobodon carcinophagus (Jacquinot & Pucheran)

INTRODUCTORY

PREVIOUS KNOWLEDGE OF THE SPECIES

THE synonymy of the species has been adequately dealt with by Allen (1905), and by Barrett-Hamilton (1902). Allen (1905, p. 92) remarks: "The species was first made known through the publication of Jacquinot & Pucheran's plates of mammals in the 'Atlas of Zoology' of the *Voyage au Pole Sud et dans l'Océanie*, which appeared at various dates between 1842 and 1853." The specimens named and figured in the 'Atlas' were derived from Dumont D'Urville's antarctic voyage of 1837-40.

Twenty years earlier, however, the scientists of Bellingshausen's Expedition had seen the Crabeater seal. A very recognizable animal of this species is figured, but not named, in the *Atlas of the Voyage of Captain Bellingshausen in the South Pacific Ocean and Round the World in the Years 1819-21* published in 1831 at St. Petersburg. Mikhailov was the artist, but there is no mention of his name on the title page. Plate 20 of this 'Atlas' shows a Crabeater and a Leopard, and another seal less certainly identifiable.

Knowledge of the Crabeater was for many years based mainly upon the writings of Barrett-Hamilton (1902) and Wilson (1907). Recently a short paper by Lindsey

¹ The above figures may be compared with Chapsky's (1936) conclusion for the Walrus of the Kara Sea. He considers that 18-20 per cent of the yearly crop of pups die in each of the first and second years, while the males and females are sexually mature in their sixth and fifth years respectively.

(1938) has appeared which makes the first real attempt to describe the growth and development of the animal. Lindsey's work on the species was, however, definitely subordinate to his work on the Weddell seal.

In Graham Land, from 1934 to 1937, 177 Crabeater seals were killed as food for men and dogs, this being about half as many individuals as of the Weddell. As with that species, every opportunity was taken to obtain as full data as possible, but the appearance of the Crabeater inshore in large numbers unfortunately coincides with the open water navigation period. This coincidence was a very real factor in reducing the possibility of complete observations being made.

DISTRIBUTION

The Crabeater seal is by far the most abundant of the four species of truly antarctic seals, if the whole area be considered. It resembles the other species in being circumpolar. It is essentially an animal of the pack-ice, and at least semi-gregarious in its habits. The normal northward distribution of the animal probably coincides with that of the limit of pack-ice, while to the south it extends as far as the open water reaches in summer. To the north of the region of pack-ice a few stragglers have from time to time been recorded: for example, at the mouth of the River Plate (Berg, 1898), and on the coasts of Australia (Hall, 1903) and New Zealand (Oliver, 1921). R. A. Falla (private communication) states that at least one or two Crabeaters are reported each winter in New Zealand, between May and October, and the same is probably true of Tasmania.

In view of its wide, circumpolar range, it is probable that the Crabeater is the most abundant of all the Pinnipedia, though clearly no absolute assurance is possible on this point. The only species that could possibly rival the Crabeater in point of total numbers is the Harp (Greenland or Saddleback) seal of the North Atlantic and Arctic Oceans.

MIGRATION

Whether the Crabeater seal can truly be called a migratory animal is still doubtful. It is quite certain, however, that large numbers of individual actively change from one locality to another at certain seasons of the year in some, if not in all, parts of the antarctic area. Wilson (1907, p. 33) stated: "There is, at present, but slender basis for saying that *Lobodon* is a migratory seal in any sense, but it was noticeable that so long as open water was within a mile or two of our winter quarters, we were occasionally visited by this seal, whereas it entirely disappeared and was not once seen when and so long as 5 or 10 miles of solid ice separated us from open water; although *Leptonychotes*, as I have already shown, was almost as abundant as before." Lindsey (1938, p. 457) remarks: "The mature seals concerned with reproduction remain for the most part in the pack throughout the summer. On the other hand, many of the season's young make their way towards the continental coast in December or perhaps earlier, and constitute two-thirds of the number found in summer in the Bay of Whales. . . . It appears that the southward movement to the antarctic coast in the spring and the return to the pack-ice in the autumn involves chiefly young

individuals. It is yet to be determined whether this movement is characterized by sufficient regularity and general participation to justify the term 'migration'."

CRABEATER SEALS KILLED IN GRAHAM LAND

1934-37

1935												
<i>Sex.</i>	<i>Jan.</i>	<i>Feb.</i>	<i>Mar.</i>	<i>Apr.</i>	<i>May.</i>	<i>June.</i>	<i>July.</i>	<i>Aug.</i>	<i>Sept.</i>	<i>Oct.</i>	<i>Nov.</i>	<i>Dec.</i>
Males ..	0	12	13	16	6	0	0	0	0	2	1	2
Females ..	2	4	4	10	9	1	0	0	0	1	1	1
? sex ..	2	1	4	2	1	0	0	0	0	0	0	0

	1936												1937					
<i>Sex.</i>	<i>Jan.</i>	<i>Feb.</i>	<i>Mar.</i>	<i>Apr.</i>	<i>May</i>	<i>Jun.</i>	<i>July</i>	<i>Aug.</i>	<i>Sept.</i>	<i>Oct.</i>	<i>Nov.</i>	<i>Dec.</i>	Shore			Ship		<i>Totals.</i>
Males	14	9	4	0	0	0	0	0	0	0	0	0	0	0	4	2	1	86
Females	19	8	6	0	0	0	0	0	0	0	0	4	0	1	7	0	1	79
! sex ..	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
																		177

On the west coast of Graham Land the appearance is more truly that of a real migration. Here, owing to the configuration of the country, the movement seems to be more nearly east and west than north and south. Seals were killed for food roughly in proportion to their abundance at the time. The table above showing the numbers of Crabeaters killed in different months of the year therefore gives directly a measure of their presence or absence in inshore waters at the different seasons. It is clear from this alone that the months of January, February, and March (April and May as well in the more northern area around the Argentine Islands), were those when Crabeaters were inshore, while in the other months of the year they were virtually absent from the coast. It is to be remembered that on the west coast of Graham Land, particularly in its northern parts, there is a general tendency for the ice to drift away from the coast in summer. The appearance of the Crabeater seals in summer in this region cannot, therefore, be due to a passive drift of seal-bearing floes into inshore waters. The influx of these seals near to the coast was extremely sudden and well-marked. In January 1936 at the Argentine Islands, when the conditions of observation were best, the influx took place in the first few days of the year. The animals that appeared at that time were not obviously the younger seals as was apparently the case in the Bay of Whales. At this time groups of a dozen or so Crabeaters were frequently to be seen swimming in company in rapid and apparently purposeful manner among the islands. Even on their first

arrival the animals to a large extent had to make use of low, weathered bergs and bergy-bits, rather than true floes, for lying out purposes.

The disappearance of the Crabeater seals in autumn was a much more gradual process, and took place by almost imperceptible degrees during the period of formation of the winter ice. In the present writer's view it is probable that, when there is a greater knowledge of the animal spread throughout the year, it will be necessary to class the species with the truly migratory seals.

In his private diary of the voyage and drift in the Weddell Sea, Worsley¹ makes a number of remarks that have a direct bearing on this subject. On 10/1/15 land had been sighted (noon position: 72° 02' S., 26° 12' W.) and on that day "hundreds of Crabeaters" were seen, after small numbers only in the preceding days. On 11th again there were "many Crabeaters. Passed two schools of Crabeaters swimming fast to the north; beginning of a great migration of seals from the south." The next day (14th: 74° 09' S., 27° 16' W.) he remarks upon "many packs of 20 to 60 Crabeaters swimming from the barrier to the pack, but appear to be making to the north." On 16th (76° 27' S., 28° 51' W.) there were "very many Crabeaters". On 17th in almost the same position there were "several Crabeaters". The *Endurance* was beset on 18th, and thereafter the number of seals was small until 9/4/16. On that date in 61° 56' S. and 54° 05' W., the *Endurance* people "took to the boats" and saw "many Crabeaters". On 10th and 11th there were "numerous Crabeaters", while on 12th (62° 15' S., 53° 17' W.) there were "Crabeaters in countless numbers on pack, especially at the edges".

The interpretation of these movements of Crabeaters described by Worsley is not yet clear, but they go far to bear out the supposition that the species is truly migratory.

INTRODUCTORY DESCRIPTION OF LIFE AND HABITS

The Crabeater seal is, as stated above, essentially an animal of the drifting ice. It very rarely lies out on rocky islands or beaches, but sometimes may be seen on snow patches when such are only a short distance from the water's edge. At all times, so far as is known, the animal tends to be gregarious. In the summer season in inshore waters, small floes or bergy-bits are often crowded with the animals, although there are plenty of other apparently suitable pieces of ice on which they might haul out.

The Crabeater seal is a far more lithe and active animal out of water than is the rather slug-like Weddell. This difference in 'condition' is also very noticeable when members of the two species are cut up shortly after being killed. In distinction to the Weddell, which progresses on land solely after the manner of a looper-caterpillar by alternate jerkings forward of the pelvis and pectoral regions (see Wilson's vivid description 1907, p. 20), the Crabeater seal can, in addition, progress rapidly over the ice or snow by a swimming motion of the hind part of the body. Wilson (1907) describes this type of progression very adequately, while Lindsey (1938, p. 459) bears eloquent testimony to the speed and endurance of the animal out of the water,

¹ The writer is indebted to J. M. Wordie for the loan of a typescript of the zoological material abstracted from Commander Worsley's private diary.

stating that: "He [i.e. Paul Siple] kept the seal from greatly lengthening its lead only by sprinting at full speed over the hard-packed snow surface, and this continued for over one-half-mile . . ."

The normal diet of the Crabeater seal consists entirely of Euphausiids, and this food gives the characteristic pink coloration to the faeces. The colour of the seal in the summer is a bleached silvery-white (hence the older term 'White seal'), which is moulted in the autumn to give place to a mottled grey-brown coat. The animal, when adult, usually reaches a length of about 95 in. from nose-tip to tail-tip. There is a small tendency, as in the Weddell, for the female to reach a rather greater length than the male.

Owing to the circumstances of its life on the pack-ice, the Crabeater seal has remained practically unobserved and unknown except in the summer months, when it has moved to inshore waters. Knowledge of its habits and breeding behaviour in all but the summer months are therefore based very largely on deduction and analogy. It is clear that the Crabeater pups at roughly the same time of year as the Weddell seal, in the very early spring, but it does so on the pack-ice far from the coast. The pups are almost unknown, having been observed (and then only stray, single individuals) only by the members of the *Belgica* and *Endurance* Expeditions when their ships were beset in the pack-ice of the Bellingshausen and Weddell Seas respectively. Most unfortunately, the information derived from these two opportunities for observation is extremely scanty and fragmentary.

In the course of the work in Graham Land calculations were made from foetal sizes to determine the time of pupping. It was then hoped that at the appropriate season a flight by aeroplane might be made over the pack-ice in an attempt to find the breeding animals. Unfortunately in both seasons, for technical reasons, this project proved impossible of fulfilment.

According to the information available, the pup, when born, remains on the ice, attended by its mother, for 3 or 4 days only, and then enters the water and fends for itself. Copulation takes place near midsummer and the period of gestation is about 9 months. Besides being precocious compared with the Weddell in the shortness of its lactatory period, the young Crabeater apparently grows much more rapidly, and the females may become pregnant for the first time a month or two after they are one year old. The female Crabeaters, or some of them, thus pup at the end of their second and subsequent years, compared with the first pupping at the end of the third year in the Weddell.

SPECIAL HABITS AND ATTRIBUTES

FOOD

At all stages in the life history, once lactation is over, the normal diet of the Crabeater seal consists entirely of Euphausiids.

The amount of food taken is great, and it is evident that the highly specialized filtering tooth mechanism is very efficient. The following description of the normal method of feeding is transcribed from the writer's notes made on 27/1/36 between

3 and 4 a.m. in calm, clear weather. "During anchor watch two adult Crabeaters watched feeding close to ship. Their habit was to remain roughly 3 minutes below, then return to surface for about $\frac{1}{2}$ minute, during which time they lay practically quiescent . . . with the head half out, the eyes shut, and breathing rapidly but not obviously deeply. The breathing was noisy with great dilatation of the nostrils during inspiration and expiration . . . the nostrils being closed for a moment between. The rate of breathing was about 1 breath per $1\frac{1}{2}$ seconds, i.e. 17 to 20 breaths in the approximate $\frac{1}{2}$ -minute stay at the surface. . . . All movements were done in almost perfect unison by the two seals. Before diving no final larger breath was ever taken, merely a sudden cessation of the normal rapid breaths. When diving they went each time vertically downwards until obscured at about 5 fathoms. The return to the surface was usually within 20 yds. of the place of diving."

Wilson (1907) gives a different description of the normal feeding method of the Crabeater seal, but whether it is based on observations or on surmise is not stated. He states (p. 26): "Either at the bottom of shallow seas, or at the 'foot' or submerged ledges of bergs and floes, it stirs up both mud and grit and gravel, taking these in freely with the Crustaceans that are stirred up with them. . . . The grit, however, which forms a fairly constant part of the contents of the stomach and intestines, serves, no doubt, to grind up the shells of the Crustaceans, and in this way the necessity for grinders [i.e. molar teeth of grinding type] is completely obviated." In Graham Land, on the other hand, grit was very rarely found in the gut of the Crabeater seal, a large quantity being present in one instance only, on 10/3/37. The stomach of this animal, a female 99 in. long, contained about 5 lb. of hard-packed sand, and there was a good deal of sand throughout the gut.

The whole problem of the swallowing of stones, sand and gravel by seals is still unsolved. That a large number of seals of diverse species have been found to contain large or small quantities of such material is undoubted, but there is no proof that this subserves any useful purpose, or alternatively that there is any directly harmful result. (Turner, 1888, *et al.*).

The most usual, though still rare, variation in the standard diet of the Crab-eater is the presence of a few small fish. Wilson (1907, p. 34) mentions one other case of diet variations: ". . . a single *Lobodon* made its appearance, a male, considerably battle-scarred and weather-worn. It had been freely eating a red seaweed, with which we found the stomach filled. It is possible, however, that this animal was sick, and that in thus entering the strait [i.e. McMurdo Sound] at all it was following the instinct of retirement in sickness and approaching death, upon which I have dealt more fully in speaking of Weddell's Seal."

SWIMMING AND DIVING

Certain of the general remarks made under this heading for the Weddell seal are obviously applicable to the Crabeater as well. Little can be said as to the comparable efficiency in this respect of the two species. Wilson was probably correct in believing that the Weddell is somewhat the swifter and more agile animal below the surface.

In the summer season the Crabeater, quite unlike the Weddell, is sometimes seen

swimming in small companies, with speed and apparent purposefulness, between and along the shores of islands or among the scattered floes and bergy-bits. In contrast again with the Weddell, the Crabeater has not been seen to sleep motionless at the surface. Whereas the Weddell in trying to mount on to a floe from open water will frequently make several abortive attempts before at last succeeding, the Crabeater will sometimes fling itself completely clear of the water in the first attempt and so land direct upon the ice.

As to the entry of the young seal into the water, information is scarce. We have nothing but Racovitza's (1900) assurance that this may take place within a few days of birth, when the mother leaves the pup to look after itself. Knowing, however, the way in which the young of some other species of seals (for example, the Grey seal) will enter the water prematurely if disturbed, it is difficult to feel completely convinced that Racovitza's figure is normal. The members of the *Endurance* Expedition in the Weddell Sea are the only others who have been in a position to provide information on the point. Nothing has been published as a result of their observations on the seals, but Worsley in his private diary, under the date 18/11/15 (i.e. 3 weeks after the loss of the *Endurance*), in $68^{\circ} 38' \text{ S.}$, and $52^{\circ} 23' \text{ W.}$, remarks of a female pup Crabeater that she "appeared to be less than a month old, but had lost her baby fur, which happens about 10 days after birth, after which the mother forcibly takes the baby into the sea". Whether this entry of the water at 10 days is the normal course is again doubtful. In his very carefully compiled diary of observations, Worsley included the numbers seen of all species of seals, besides those killed. But there are only 6 or 7 young Crabeaters mentioned in all, of which the case quoted above, and another 8 days earlier, are the only ones which, by his own statement, can have been less than a month old.

There is nothing inherently improbable in the young Crabeater entering the water within a very few days of birth. The pups of the Common seal are frequently born on sandbanks where they must take to the water on the day of birth (Millais, 1906; Havinga, 1933). The fact that the Crabeater is born in the usual infantile woolly coat, which is not moulted for some days, is certainly a strong suggestion that, if undisturbed, the young animal will remain at least a few days on the ice, until the moult has started. The Common seal moults the infantile woolly coat either immediately before or after birth. The Hooded seal moults the woolly coat shortly before birth, and the pups enter the water after a very few days. So far as is known all other species of True seal are born in the woolly coat and do not enter the water, unless disturbed, until after the moult at least has started.

WINTERING BENEATH THE ICE

The Crabeater seals normally leave the inshore waters of the Antarctic during the autumn, and remain in the pack-ice offshore until the following summer. However, on the west coast of Graham Land evidence was obtained showing that a small number of Crabeaters may sometimes live through the winter inshore beneath the ice, in the same way that the Weddell normally does. These few records are detailed below:

(a) 9/9/35. Berthelot Islands. An adult Crabeater thrust its head through a narrow crack in the sea-ice and at once disappeared again. At the time there was no known open water within at least 7 miles, and no other Crabeaters had been seen since the beginning of June. After 9 September no other Crabeaters were seen until patches of open water were appearing in the middle of October.

(b) 31/7/36. Half-way up Laubeuf Fjord. The ice was known to be unbroken in all directions, the nearest open water being a pool in the narrow channel some 12 miles away to the north. After the severe winds of the two previous days, a berg beset in the sea-ice had shifted by 2 or 3 ft. to leave an open crack of water. Through this 11 seals had emerged (they were not there on the previous day), 7 being Weddells (6 males, and 1 female), and 4 Crabeaters (all males). It seems certain that these Crabeaters must have been wintering beneath the ice and had taken this opportunity to emerge.

(c) 17/11/36. Marguerite Bay. A young male Crabeater emerged from a crack by a big berg. At that time there was certainly no open water within 30 miles.

(d) 6/12/36. Marguerite Bay. Two female Crabeaters, both 100 in. long, were killed near a berg a mile or so to the north of the Debenham Islands. There was no open water within 30 miles. Five Crabeaters had been seen lying out at this spot as early as 12/11/36. On 15/12/36 two more female Crabeaters were killed at the same spot, and a further 2 were seen there. No other Crabeaters were found in Marguerite Bay until the open water appeared in late January. All the 4 Crabeaters killed at this spot had markedly empty guts, suggesting that Euphausiids were perhaps absent beneath the fast-ice, and the seals had been forced to starve. Their blubber, however, showed no obvious signs of depletion.

There can, then, be little doubt that Crabeaters occasionally, perhaps through becoming embayed at the freeze-up, winter beneath the fast-ice just as do the Weddells. Whether in such circumstances they are able to obtain food is unknown: the little evidence available suggests that they may not be able to do so. No Crabeater was found whose canines or incisors showed obvious considerable traces of wear by ice-sawing as in the older Weddells, but the wear during a single season's sojourn beneath the ice would not, in any event, be great. There is always the possibility of a Crabeater being able to winter beneath the fast-ice simply by making use of the breathing-holes kept open by Weddell seals. Such an existence would be precarious but by no means impossible.

Wilson (1907, p. 36) expresses his views thus: "In a few rare cases there is seen to be some wear, however, in the teeth, and this always in the skulls of the oldest seals. Such wear is not easily accounted for, but may follow, I think, from some change in habit or of diet in old age, perhaps as in Weddell's seal, from opening ice-holes in a secluded bay, or from changing to a seaweed diet as above suggested. The delicate nature of the cusps, one might think, would lead to frequent damage, but this is not the case; and though it is quite a common thing to find grains of sand and grit wedged in immovably between them, they are very rarely broken. If in extreme old age a seaweed diet is preferred, it is possible that in wrenching this from the rocks upon which it grows, the teeth might show some such effect in wear, though one thing is certain, that in the great majority of adult skulls there is hardly any sign of wear at all."

MOULT AND COLOUR CHANGES

The moult and colour changes of the Crabeater seal are adequately dealt with by Wilson (1907). Before his detailed observations there had been a good deal of faulty identification and lack of realization of what was taking place. The main facts are that the old coat of the Crabeater weathers to a silvery whiteness before the moult. The moult of the 'White seal' takes place in the summer months (January and February) precisely at the time of year when they are most likely to come under observation. It was the transition from the more or less uniform silver colour to a somewhat mottled grey-brown (richer and more mottled and ring-spotted in the younger animals) that misled the earlier observers.

Like the Weddell seal "the moulting Crabeater neither shuns water nor prefers to starve while his coat is being shed." Wilson (1907, p. 37).

Of the moult of the natal coat in the Crabeater, extremely little is known. Worsley's diary has already been quoted to the effect that the natal coat is lost about 10 days after birth, and the paucity of evidence on which this statement is based is also noted. Racovitza is quoted by Wilson (1907, p. 35) as to the appearance of the young animal, but there is no mention of the moult. "Le jeune unique est couvert d'une épaisse fourrure de la même couleur que celle des parents, mais beaucoup plus fournie."

One young Crabeater, and one only, was seen, at Robertson Bay, by the members of the *Southern Cross* Expedition. This was on 29 11 99, a few weeks after Hanson's death, so that our knowledge is less detailed than it would otherwise have been.

NOISES

The breeding season in the True seals is usually the period when they exert whatever vocal powers they may possess. On this account knowledge of the noises made by Crabeaters is wanting. At other times of the year the Crabeater, when disturbed, indulges in nothing more than an angry hissing, produced by a forcible expiration with both mouth and nostrils widely open.

FIGHTING, WOUNDS, AND MORTALITY

Like the Weddell seal, neither sex in the Crabeater indulges in fighting to a degree comparable with that of the males in the polygynous species. But from the abundance of small scars about the head and neck, of the males in particular, it is evident that some fighting does occur, and presumably this is at its height at the mating time. The Crabeater, unlike the Weddell, seems to attack the head and neck only of the rival, not attempting to concentrate upon the axilla and genital orifice. Worsley mentions in his diary (19 10 15) a bull Crabeater that was "tremendously scarred all over . . . nearly all the marks on the shoulders appear to have been the results of seal fights: but he also bears several of the long scars that testify to some exciting escapes from Killers."

Rudmose Brown (1913, p. 195) remarks: "A peculiarity of the *Lobodon* is the scarred appearance it presents in midsummer. In December this is most noticeable;

in January their condition improves, and in February as a rule, they are free from scars. . . . The fact seems to be that these scars are inflicted in November and December . . . ; this coincides with the rutting season, when no doubt the males are badly wounded in fighting with one another. As far as the observations of the *Scotia* naturalists go, the scars are confined to the males; but in 1892 Dr. Bruce comments on the females being as badly scarred as the males." In Graham Land too the females were far from being clear of the scars, though certainly bearing fewer of them.

The small wounds and scars about the fore part of the body are always very clearly distinguishable from those great raking cuts, usually ventro-laterally situated, that are such a feature of any group of Crabeater seals, the result of attacks by Killer whales. In this connection it has been pointed out that the Weddell is almost free from such attacks, owing to its inshore habits. In the various accounts of the sealing exploits of the Dundee whalers in 1892-93, it is clear that on that occasion the great majority of the Crabeater skins were marred by the presence of these scars and gashes. The cuts inflicted by the Killers vary from a few up to 20 in. in length, and most usually occur in pairs, the two parallel cuts being 2 to 2½ in. apart. It is clear in most instances that the attacks have come from behind and below, the resultant wounds running from a dorso-lateral position backwards and downwards at an angle of roughly 45° to the long axis of the body. This is the most usual situation of the wounds, but is by no means the only one. Worsley describes a Crabeater (2/10/15) with half of one of the flippers (whether fore or hind is not mentioned) torn away, and having in addition the scars of extensive wounds.

In the Graham Land waters very few Crabeater seals were seen that were quite free from these immense wounds. Even the young seals, only a few months old, very frequently already bore the marks of the Killer whales' teeth. In the Bay of Whales, Lindsey (1938) apparently found a somewhat different state of affairs. His observations showed that about two-thirds of the Crabeaters seen in the summer months were young animals, born early in the same season, that had migrated south from the main Ross Sea pack at the age of a few months. He states (p. 457): "The best evidence," that these were season's young, "is found in their freedom from scars. The presence of long parallel scars from the teeth of the Killer whale (*Orca*) is the general rule among adult Crabeaters. In the days of antarctic sealing it was found that about one-half the Crabeaters taken were so badly scarred in this way as to be worthless commercially. It is a striking fact that the great majority of this species in the Bay of Whales were completely free from old scars, although fresh gashes were commonly seen. These wounds were of the long, raking type inflicted by the Killer, and had probably been incurred during the trip through the open Ross Sea from the band of pack-ice to the Bay of Whales. The absence of healed scars on the skins of the youngest age group in the Bay strongly indicates that these were seals of the year that were born only 6 months previously in the pack."

The abundance upon the body of the Crabeater of these Killer whale tooth-marks is a clear indication of the frequency of attack. What proportion of attacks results in the death of the seal is quite unknown, but one would suppose it to be rather small. If it were not so, it is difficult to understand how the seal could be so abundant and yet almost every individual possesses on its skin the permanent marks of at least one such attack. Even so it is probable that these attacks are the chief

cause of mortality in the species, which, judged by the standard of the Weddell seal, is extremely free from disease. Thus it is highly probable that most Crabeater seals eventually meet their death at sea. A few, however, clearly die otherwise, as is shown by ancient individuals wandering inland far away from the sea. A number of such cases have already been described in the section dealing with mortality in the Weddell seal.

An injury suffered by one animal in the Graham Land series of Crabeater skulls is worthy of particular mention. Skull No. 11 (unsexed, but almost certainly an old male), has the left mandible broken through at the level of PC 4. The break is evidently of some age, but no pseudo-arthritis has been formed, and the amount of necrosis has been surprisingly small. No other skull in the series of either sex has suffered important injury.

DENTITION

The foetal material available for the study of the milk dentition in the Crabeater is less extensive than in the case of the Weddell. There is, however, nothing to show that the milk dentition in the Crabeater follows any course other than that found in the Weddell. Crabeater and Weddell foetuses of approximately the same size are extremely similar in the stage of development of the milk teeth, and what has already been said for the one may be taken to apply equally to the other. In the milk dentition of the Crabeater the upper last pair of post-canines shows a small amount of cusping, so foreshadowing the complicated arrangement that is found in the permanent cheek teeth (plate III).

As to the stage of development of the teeth at birth, Racovitza states (as quoted by Wilson (1907, p. 35)): "Le bébé, au moment de sa naissance, a une taille considérable; 1-15 mètre; il possède déjà des dents et des yeux parfaitement fonctionnels et même une couche de graisse sous-cutanée efficace pour le protéger du froid. Il peut donc immédiatement se tirer d'affaire tout seul; aussi la mère l'abandonne-t-elle après l'avoir allaité seulement deux ou trois jours." On the other hand Worsley, in his diary of 18/10/15, remarks of a young female Crabeater that she "appeared to be less than a month old, but had lost her baby fur, which happens about 10 days after birth . . . The calf's stomach was absolutely empty and clean and baby teeth just beginning to develop the cusps." Worsley's description is not very precise, but it is clear that the young animal's teeth were not truly functional at that time. There are no skulls of very young Crabeater seals available upon which a judgment might be made. The most immature skull that has been examined is that of a young female 68 in. long from Graham Land, taken at Deception Island on 17 January 1936 (Skull No. 111). This animal was in good condition, well-blubbered, and bore no scars or fresh wounds, but the stomach was completely empty. In the intestine, however, there was a single large tapeworm some 3 ft. in length, which in itself is presumably evidence that the young animal had fed for itself for some considerable period. The teeth are in such a condition that one would suppose them adequately functional, but have by no means completed their eruption. The upper canines and incisors, for example, run more nearly parallel with the long axis of the skull than at right-angles to it, as in the adult; the lower canines are scarcely larger than the outer

pair of lower incisors; and, more important doubtless from the feeding point of view, the cheek teeth still have their lower cusps partly hidden within the sockets, this being particularly so with premolars 1 and 2 in the upper jaw, and premolar 1 in the lower. But there can be no doubt that the post-canines in general already form a satisfactory filtering mechanism. This 68-in. female Crabeater was clearly from 3 to 4 months old and its tooth condition leads one to accept Worsley's description of the very young animal as being more accurate than Racovitza's. It is highly probable, however, considering the apparent shortness of the lactation, that the teeth in the Crabeater at birth are considerably more advanced than those of the Weddell. But it would also appear that the change from the condition at birth to complete eruption is longer in the Crabeater. For example, the teeth of a young female Weddell (56 in. long) and probably 3 months old (Skull No. 84, 12/12/35) are more nearly in the adult condition than are those of a young female Crabeater a month older and 68 in. long (Skull No. 11, 17/1/36). In the young Crabeater skulls up to the age of 5 or 6 months, sometimes rather less, sometimes more, it is usual for the roots of the upper canines and the fifth upper cheek teeth (and sometimes the fourth as well) to break through to the dorsal surface of the premaxillae and on to the orbital surface of the maxillae respectively. Such a condition has never been observed in even the youngest Weddell skulls.

As to the teeth in the adult Crabeater, Wilson (1907) has already been quoted to the effect that the Leopard and Crabeater seals are remarkable in showing no tendency whatever to vary from the normal type with PC 5/5. In the Graham Land series of skulls there is a single example of tooth multiplication: a fully adult female (Skull No. 132) with otherwise normal teeth possesses on each side of the upper jaw a rather small supernumerary post-canine behind the normal fifth. Apart from this single case of multiplication, the series of Crabeater skulls available is extremely free from dental abnormalities, if the Weddell is taken as the standard. There is a slight variation in the distance apart of the cheek teeth from one another, of the tooth sizes, relative and absolute, and of the number of cusps, but these must be considered in the light of normal variations rather than as peculiarities.

The number of cusps of the cheek teeth is somewhat variable, but most usually there are three behind and one in front of the central point in each tooth, both in the upper and the lower jaws. The cheek teeth are smallest anteriorly, biggest posteriorly, the hindmost pair in the lower jaw usually being the largest in the whole post-canine series. With this increase in tooth-size posteriorly there is usually a slight increase in the number of cusps, which are fewer and smaller in front, more numerous and better developed behind. In one old female skull (No. 13) there is a tendency to increase the number of cusps throughout; for example, in the lower fifth post-canine there are four cusps behind and two in front of the central point. In the upper jaw, too, in this animal all the post-canine teeth are unusually thick in a direction at right-angles to the long axis of the tooth series. With this widening there is a development of small additional cusps medio-posteriorly on each tooth. This incipient supernumerary cusping (in No. 13) is also seen even in the upper second pair of incisors, and to a lesser extent in the upper canines.

The normal variation in the size of the incisors in the Crabeater seal parallels this feature in the Weddell. The lower incisors are almost always small and subequal,

but the outer pair tend to be the larger. These lower incisors are frequently lost either in life or in the preparation of the skull. The inner pair of upper incisors is almost always as large as, or larger than, the second pair of lower ones, and is more rarely lost. The second pair of upper incisors is larger and more caniniform, but never so nearly equal in size to the canines as is sometimes found in the Weddell. The lower canines are intermediate in size between the second upper incisors and the upper canines.

The rarity of obvious wear of any of the teeth of the Crabeater has already been commented upon in considering the food of the species, and the occasional wintering below the fast-ice. In no case has there been obvious breakage of a post-canine tooth in the Graham Land series of skulls. In only four skulls in this series has a post-canine tooth been lost in life; these cases are No. 88 (female) and No. 11 (unsexed, probably male) in both of which the right upper fifth post-canine has gone, No. 92 (male) in which both fifth upper post-canines have gone, and No. 93 (male) in which the left upper third post-canine has disappeared. In all these cases, so far as one can tell, the teeth have been lost through falling out with age, and not by fracture. Skull No. 93 (male), from the complete fusion of all the palate sutures (except the extreme posterior part of the median suture between the palatines), may be judged the oldest in the Graham Land series. The dentition of the lower jaw is perfect but for the loss of the inner pair of incisors which may or may not have taken place in the preparation of the skull. (The members of the second pair of lower incisors in this skull are curiously unequal in size.) The upper jaw, however, presents the only case of serious tooth fracture in the whole series. Both canines have been broken off short almost at the level of their emergence from the sockets; the right outer incisor has also been broken off, but within the socket, while the left second and the inner pair of incisors are all missing. In this instance it is surprising to find that no serious necrosis has taken place as the result of these fractures, whereas in the Weddell seal fractures of a far less severe character invariably seem to initiate a rapid and spreading necrosis around the injured part. It would seem that in the Crabeater, injury of the teeth is very rare, and that when it does occur the results are far less serious than in the Weddell seal.

REPRODUCTION

Knowledge of this subject in the Crabeater, for reasons already explained, is far less complete than in the Weddell seal. It will be most convenient, none the less, to follow the natural order of events as has been done for the Weddell, setting down under each heading the extent of present knowledge, and drawing what deductions are warranted, where necessary with the help of analogy.

COPULATION AND THE PRODUCTION OF SPERM

The literature mentions no case of copulation having been observed, nor was it seen in Graham Land. There is little doubt that, as with the Weddell and the majority of True seals, this occurs in the water. Worsley (in his diary for 26/11/15) mentions a possible case of copulation but gives no hint as to whether it was in the

water or on the ice. He says "two Crabeaters were seen fighting or copulating, apparently the latter, though this seems very early in the season."

The presence of sperm has been investigated by sectioning portions of testis of three males taken at the Argentine Islands, with the following results:

1237.	22/10/35.	86 in.	Skull No. 63.	(First Crabeater of season). Plenty of sperm present.
1257.	22/11/35.	86 in.	—	Plenty of sperm present.
1339.	1/1/36.	81 in.	Skull No. 91.	No sperm present.

In the case of 1339 there is some doubt as to whether the animal is sexually mature. From skull comparisons it is certainly a 'young' adult, and is very probably only 15 months of age. It is clear, however, that in October and November plenty of sperm was available. In the Weddell three males in January all had no sperm, so that quite possibly by analogy the 81-in. Crabeater described above was simply going out of breeding condition, sperm production having already ceased by that date.

Worsley's possible record of copulation in the Weddell Sea was on 26 November. Rudmose Brown (1913, p. 195) from his observations in the South Orkneys says: "the fact seems to be that the scars are inflicted in November and December . . . this coincides with the rutting season . . ." There is no statement in the text, however, that copulation was seen, and this dating of the rutting season is probably based on surmise.

GESTATION AND THE GROWTH OF THE FOETUS

In the previous section the knowledge as to the probable time of copulation in the species has been set out. Racovitza (1900) saw a few new-born pups in the Bellingshausen Sea in September. Wilson (1902, p. 75) quotes Bernacchi to the effect that "the only young of this seal procured by the *Southern Cross* Expedition was the specimen killed near its mother in Robertson Bay on 29 November 1899. . . . It was by no means so far developed as the young Weddell's seals which were quite common." One of Racovitza's pups was 45 in. long. The pup described by Bernacchi was 59 in., a measurement probably taken from nose-tip to the hind end of the back flippers, and the pup was already well advanced in its moult. The few Crabeater pups seen by the crew of the *Endurance* were seen in October, shortly after the loss of the ship. Lindsey (1938, p. 457) makes the statement: "Breeding hundreds of miles farther north, it produces its young about 1 month earlier than the mean date for the birth of the Weddell seals in the Bay, which was 24 October. . . . Since the gestation period is probably 10 or 11 months, the mating season follows soon after the birth of the young in the pack-ice." Lindsey's statements are based on surmise, using Racovitza's record of September births in the Bellingshausen Sea. It has already been seen that the Weddell seals in the Ross Sea are a month later than those in west Graham Land, so that the possibility of somewhat different pupping dates of the Crabeater in the two areas is by no means remote.

If now the graph of foetal sizes at different dates, constructed from the Graham Land data, be examined (fig. 1), it is seen that the Crabeaters in that area seem to be

about a month later than the Weddells in reaching the same foetal length. Both species apparently pup in September (in this region) so that unless the very early development of the Crabeater foetus is markedly slower than that of the Weddell, the gestation of the Crabeater must be shorter by about a month. Thus it is probable that the gestation of the Crabeater seal is 9 months. If this be so the mating season in Graham Land must be in the middle of December, a very short time before the summer influx of Crabeaters to the inshore waters takes place. It is not unreasonable perhaps to suppose that the two processes have some chronological and causal connection.

The graph of foetal sizes suggests, however, that a few Crabeaters become pregnant rather before the majority. For example, a foetus 22 cm. long, taken on 10/2/35 at the Argentine Islands, was probably at least a month older than the majority at that date. If now the ovarian data for the Graham Land Crabeaters be examined, it is seen that small embryos about 1 cm. in length were found in the early days of February. In the discussion under this head for the Weddell seal, it has been suggested that probably the embryo takes at least a month to become 1 cm. long, and that during this period the embryo would probably be overlooked in hasty butchery, and the seal stated to be 'not pregnant' unless a special search of the uterine wall were made. From female Crabeaters there are 6 pairs of ovaries taken at dates earlier than the beginning of February, when the embryos about 1 cm. long were being found. All these 6 pairs of ovaries (dated 22/11/35, 5/12/36, 15/12/36, 28/12/35, 1/1/36 and 1/1/36) were put down in the original field notes as coming from seals that were 'not pregnant'. When these 6 pairs were sectioned, each was found to possess an apparently functional corpus luteum. The sizes of these corpora are graded from about $1\frac{1}{4}$ to $2\frac{1}{2}$ cm. in longest diameter, the increase of size running parallel with the lateness of date. From these facts it seems highly probable that these 6 female Crabeaters were actually just pregnant, but the embryo in each case was still so small as to be missed in the absence of careful splitting and searching of the uterine horns.

In conclusion, all the evidence points to the Crabeater seal in the Bellingshausen Sea and western Graham Land having a period of gestation of 9 months, pupping in September and copulating in December, though sometimes copulating as much as a month earlier.

SEX RATIO, LACTATION, AND INCREASE OF WEIGHT

Nothing is known of the habits of the female Crabeaters at parturition. There is no evidence that there is ever more than one pup at birth; certainly twin foetuses have never been recorded in this species.

There is no evidence that the sex ratio is other than equality. The foetuses that were preserved and were old enough to be determined in this respect were 2 males and 3 females. As the table shows, the Crabeaters killed were 86 males and 79 females. Only if the habits of the two sexes in the summer months are precisely similar will the numbers represent a true sample of the population. Whether this is so or not remains unknown.

Lactation is probably rather short. The only facts from which conclusions may be drawn have already been quoted. Racovitza's (1900) statement that the pups

must fend for themselves as soon as they enter the water at the age of a few days is based on insufficient evidence. It would be extremely difficult to prove whether or not the mother and pup haul out at intervals and lactation continues. By analogy with other True seals (where also the information is really very scanty) the precocious moult and entry of the water by the Crabeater strongly suggests a shorter lactation period than in the Weddell. The length of the period must remain surmise until the opportunity comes of studying the Crabeater in its breeding areas.

Likewise nothing is known of the growth rates of the pups, in their first 3 months, other than what can be deduced from knowledge of the growth after this period. Clearly, however, in the first 3 months the growth must be extraordinarily rapid, the animal even reaching a length of 6 ft. or more by the end of this period. The Weddell reaches but 5 ft. approximately at the end of the first 3 months, despite the enormous percentage increase in weight during lactation. The Crabeater pup at birth, so far as the evidence goes (Racovitza's measurement of 45 in.), is rather smaller than the average Weddell pup.

The Crabeater pup at birth probably weighs about 50 lb. Measured weights of older animals are few. Bruce (1915, p. 574) gives data from 4 animals.

<i>Date.</i>	<i>Sex.</i>	<i>Body Length.</i>	<i>Weight.</i>
2/2/03.	Male.	88 in.	4 to 5 cwt.
10/2/03.	Female.	81½ in.	c. 300 lb.
3/3/03.	Male.	98 in.	494 lb. (Blubber 147 lb. Skin 47 lb.).
1/8/03.	Male.	—	325 lb.

The 98-in. male at 494 lb. may presumably be taken as the approximate weight attained by adult Crab eaters, and this may be compared with a 100-in. male Weddell that weighed 787 lb. As already stated, the Crabeater is a much more lithe and slender animal than the Weddell, and it is not unlikely that a 5-ft. Weddell at 3 months of age might weigh as much as a 6-ft. Crabeater at the same age. This consideration brings the growth of the two species in the first few months more nearly into line.

The average blubber thickness of the Crabeater seal, as seen inshore in the summer season, is about 2 to 2½ in. over the major part of the body. It was never seen quite as thick as in the thickest Weddells.

GROWTH AND AGE

Possible methods of determining the ages of individual seals have been considered fully under this heading for the Weddell. For the Crabeater the same methods and arguments are used in the following sections, in an attempt to find the composition of the population, just as has been done for the Weddell. The Crabeater data are, however, in all respects somewhat less complete.

BODY LENGTH

The data suggest that, as in the Weddell, so in the Crabeater, the females tend to reach a rather greater length than the males. Using the only two long series of

measurements available, in Lindsey's (1938) figures there are two females longer than the longest male (i.e. females of 94 in. and 96 in., and a male of 92 in.), and in the Graham Land figures, though there is only one female longer than the longest male (i.e., a female of 103 in., and a male of 101 in.), there are seven further females longer than the second longest male (i.e., 4 at 100 in., 2 at 99 in., and 1 at 97 in., the male being 96 in.). The sexual disparity in size of the Crabeater is thus of about the same order as that in the Weddell, and in the same direction.

After seeing hundreds of Crabeater seals, it was concluded that no certain sex distinction could be made on general appearance. As explained above, the longest seals may be expected to be females, but this is of little use in determining the sex of the 'average' animal when adult. Sometimes the males could be distinguished by an apparently larger head and the greater abundance of scars about the head and neck. On the whole these older bulls tended to show a greater fierceness towards man. The Crabeater seal is, however, extremely variable in this respect, sometimes continuing to lie practically quiescent or move slowly away when approached, at other times making short rushes towards the intruder. Single animals usually tend to resist approach more than do the members of a group. Sometimes one can land on a floe 10 yds. in diameter and shoot six out of a dozen seals, without the others paying anything more than a cursory interest in the proceedings.

Lindsey (1938) made an attempt to separate the age groups of the Crabeater by the consideration of the body lengths of 61 animals killed in the Bay of Whales between 9 February and 14 March. His figure based on these measurements is here reproduced in its original form (fig. 30, A), and in addition, separated into its male and female components (fig. 30, B and C). He states (p. 457): "Since the measurements were all taken within about one month, the drop to the base line at the 81- and 82-in. column (except for one seal 81 in. long) separates the season's young from those in their second year. The season's young of the Weddell seal had not exceeded 75 in. by the middle of March, but the Crabeater is more precocious in several respects." He goes on to say: "Forty-two of the 61 individuals measured were less than 1 year old. Analysis of measurements of four dimensions throughout a series of 32 Crabeater skulls, taken at the same time of year, led to a corresponding conclusion . . ." He then proceeds to the statements already quoted concerning the fact that the young animals of the season are also distinguished by the absence of healed scars on their bodies (p. 458). "The frequency data in figure 1 [i.e., fig. 30, A] furnish evidence regarding the age at which these seals begin to breed. The occurrence of embryos is indicated by 'em' for each length class represented by females containing embryos. The smallest pregnant females fall in the column immediately after the hiatus between the first two age groups. It follows that the females may mate at the age of only 1 year and 1 or 2 months, and bring forth their first young when they are just 2 years old. This is 1 year earlier than in the Weddell seal . . . but the discrepancy seems less surprising when the rapid development of the young Crabeater is considered. . . . In view of such a precocious infancy it seems credible that some of them swim from the pack-ice to the Bay of Whales when 4 or 5 months old, and that a female may bear her first young when she has just turned 2 years old." Beyond this separation of the young Crabeaters approximately 5 months old, Lindsey was unable to define further age classes among the seals from the body measurements.

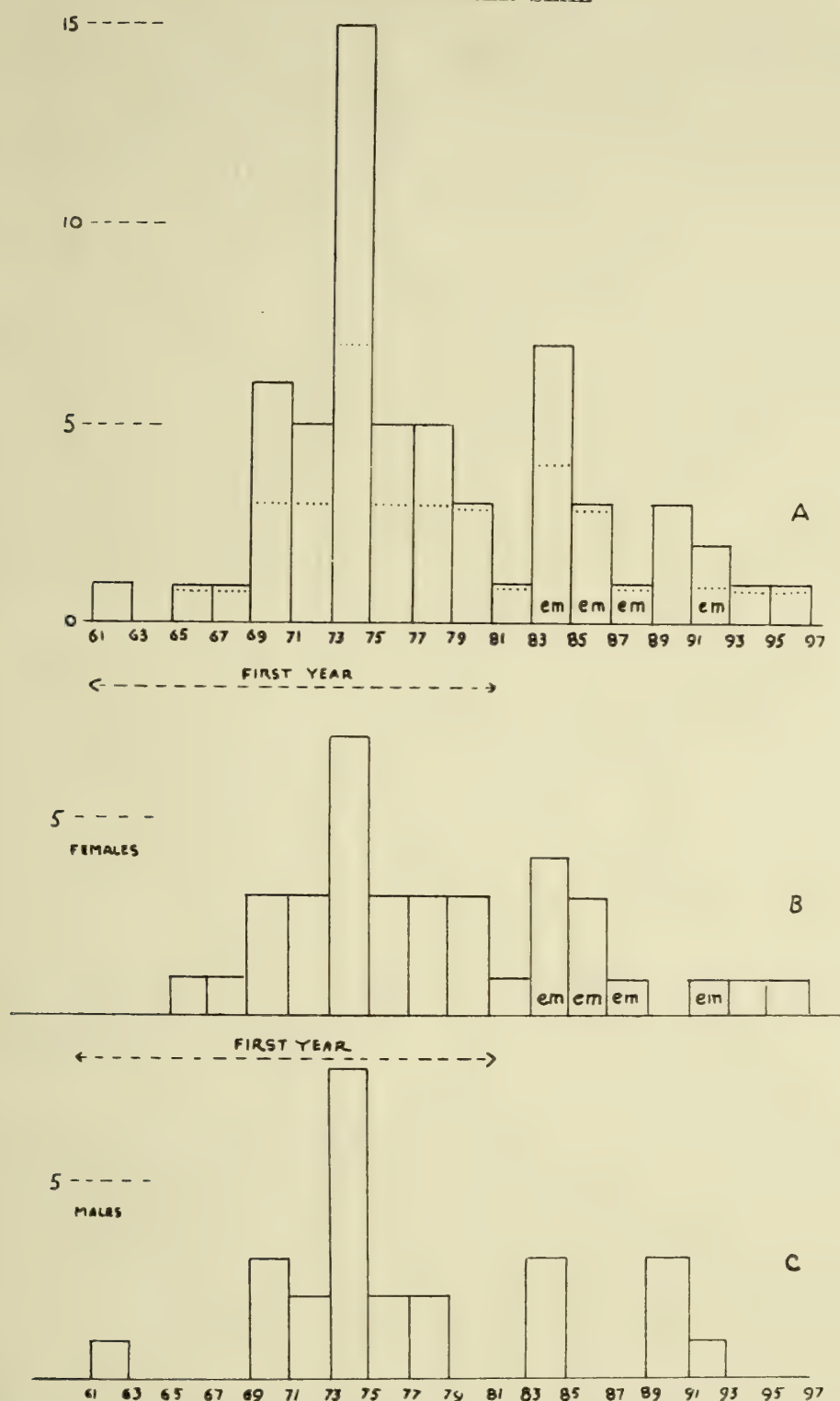


FIG. 30.—A is a reproduction of Lindsey's (1938) fig. 1, to which the legend was: "Frequency distribution of nose-tail length measurements of 61 Crabeater seals measured 9 February to 14 March. Class interval, 2 in. Males above the dotted line; females below. Ordinate, number of animals; abscissa, their lengths. Classes in which females contained embryos indicated by 'em'." B and C represent A separated into its male and female components for greater ease of interpretation.

In Graham Land it was possible to measure a rather greater number of Crab-eaters than in the Bay of Whales, namely 41 males and 62 females, but, whereas Lindsey's seals were spread over a single month, those in Graham Land are spread over rather more than 6 months. This being so, it is not helpful to set out the

BODY LENGTHS OF ALL CRABEATERS IN GRAHAM LAND SERIES.

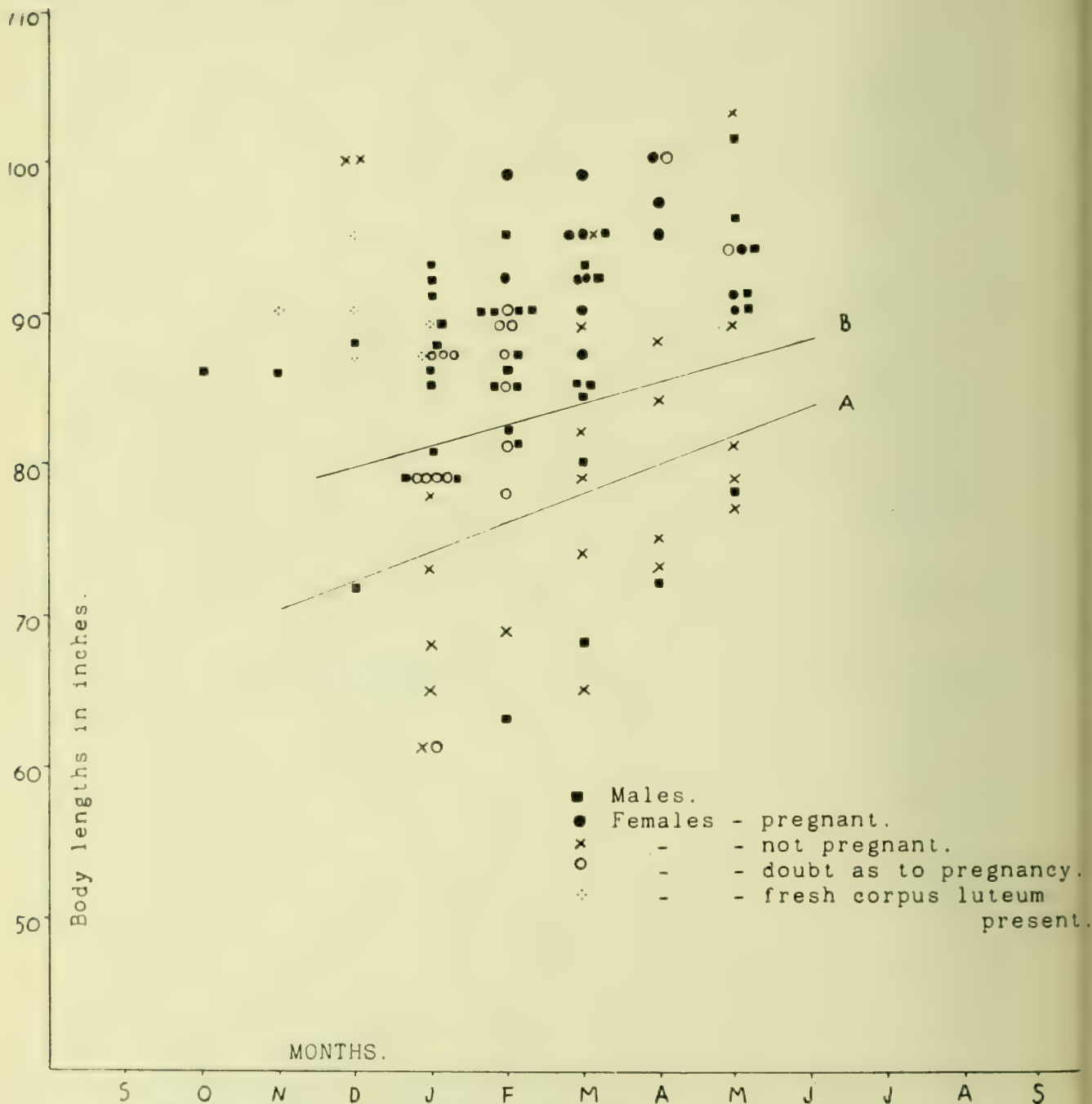


FIG. 31.—Diagram to show the body lengths of all male and female Crabeater seals killed in Graham Land month by month. A distinction is made between the several classes of female seals. The significance of the lines marked A and B is explained in the text, p. 103.

figures in the same graphical form as Lindsey uses. Instead, the figures are set out month by month, in one diagram to show males and females together (fig. 31), in another to show the sexes separately spread over the months of several years (figs. 32, 33). In the latter figure Lindsey's series of measurements is superimposed upon the month of March for the respective sexes.

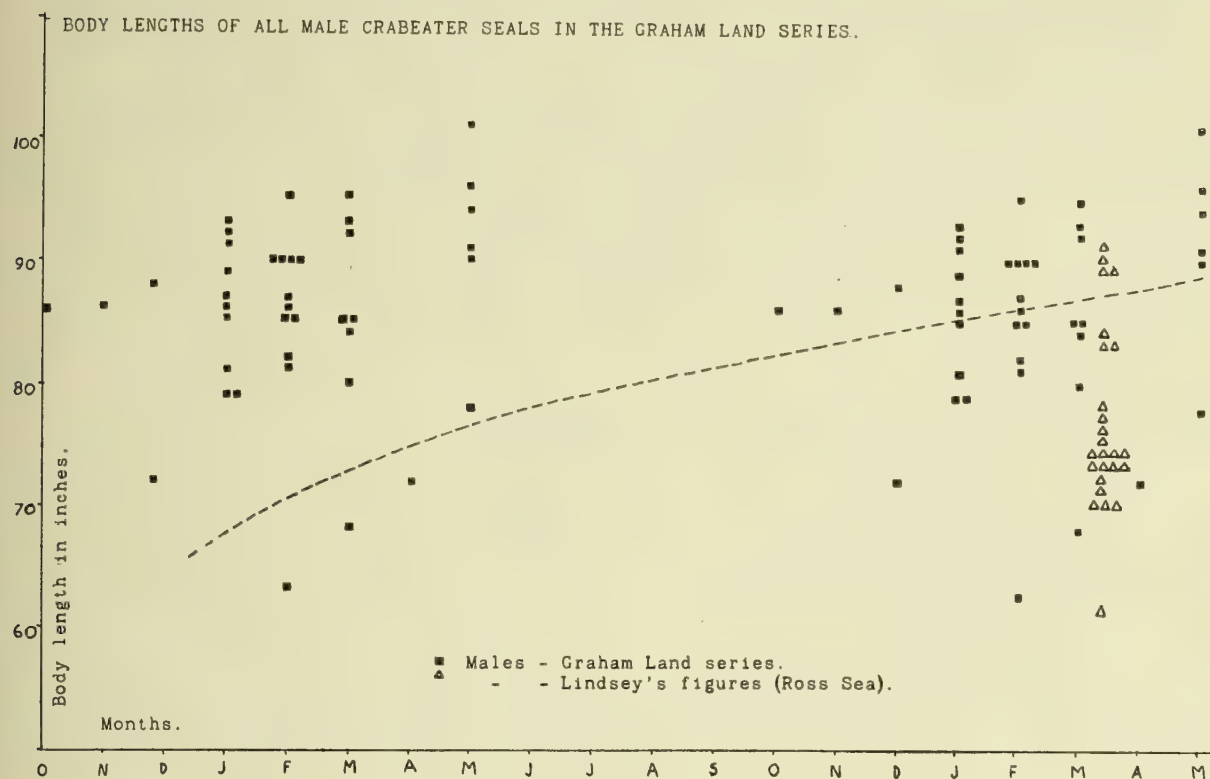


FIG. 32.—Diagram to show the body lengths of all male Crabeaters from Graham Land repeated month by month over two years to show the most probable method of growth. The lengths of the male Crabeaters taken by Lindsey in the Ross Sea between 9/2/34 and 14/3/34 are inserted for comparison.

When the Graham Land figures, or the combined series of figures, are examined, it is seen that though they are in very fair agreement, the distinction between the $\frac{1}{2}$ -year-old seals and those of greater age is not, after all, completely clear. For example, it is doubtful whether those males and females taken in Graham Land in January, February, and March that are between 78 in. and 82 in. in length inclusive, are to be included or not in the $\frac{1}{2}$ -year-old group of seals. If they represent $1\frac{1}{2}$ -year-old animals, it would seem that compared with the growth in body length during the first summer, the increase in the following winter in the pack-ice is extremely small. In the diagram (fig. 31) of the monthly lengths of both sexes of the Crabeater in Graham Land, two oblique lines have been drawn in by eye where the most 'natural' divisions seem to lie. The line marked A appears, from these figures alone, to be the most probable upper limit of growth in the first summer. The line B seems to mark a slight break in the series of measurements, and may or may not represent a true division between year groups. By comparison with Lindsey's Ross Sea

BRITISH GRAHAM LAND EXPEDITION

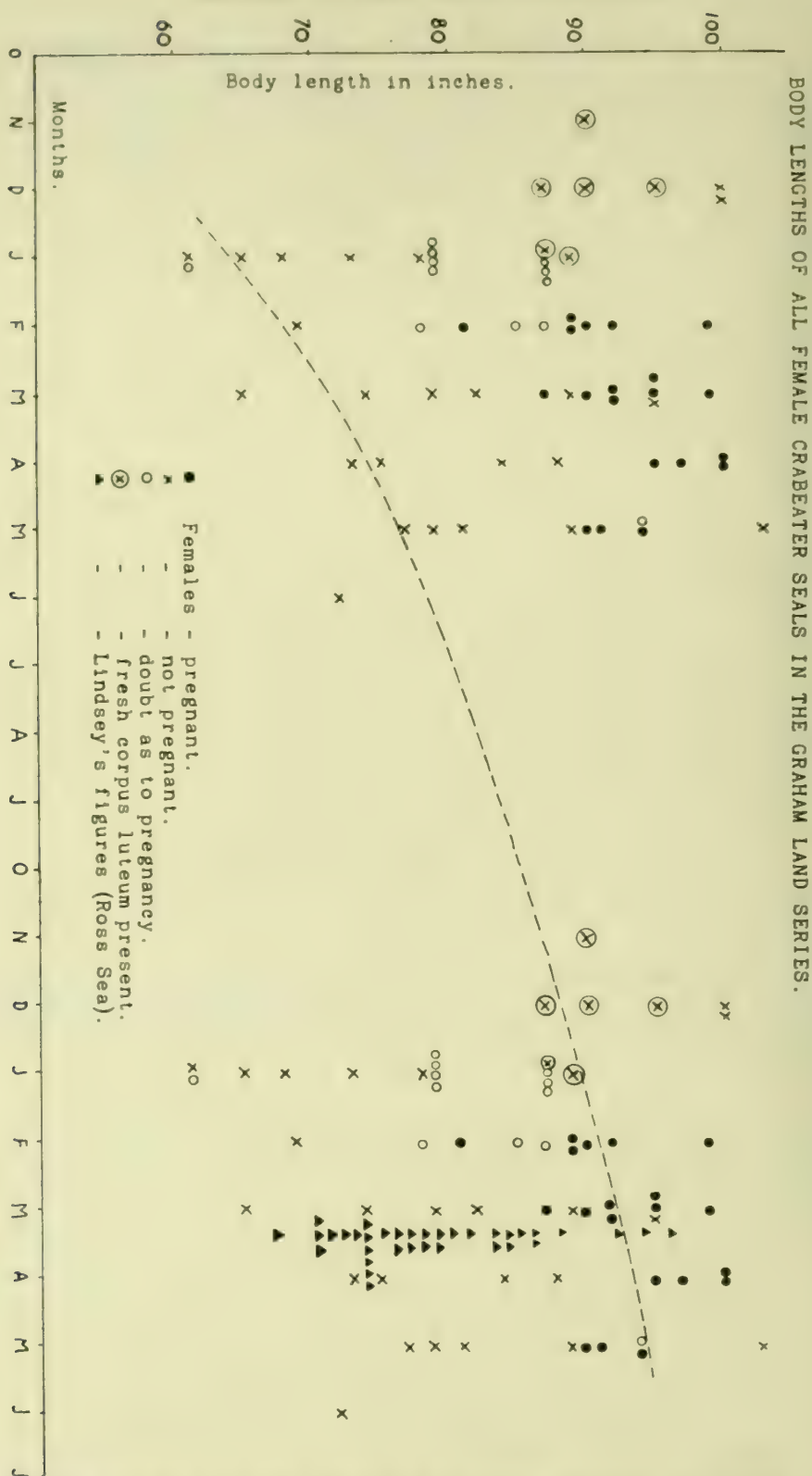


FIG. 33.—Diagram to show the body lengths of all female Crabeaters from Graham Land repeated month by month over several years to show the most probable method of growth. The lengths of the female Crabeaters taken by Lindsey in the Ross Sea between 9/2/34 and 14/3/34 are inserted for comparison.

data (fig. 30—if we assume the seals in the two areas to behave in exactly the same manner as regards length), the line B more nearly represents his separation of the first-season seals from those a full year older.

Lindsey's smallest pregnant seal was 83 in. in length. In Graham Land the smallest is 81 in. Unfortunately in this series near the critical length there are 5 females (1 at 78 in., and 4 at 79 in.) for which pregnancy data are lacking. For this reason it would be unsafe to say at once from the Graham Land figures whether the female Crabeaters do actually become pregnant when a few months more than a year old, as Lindsey has inferred.

Some better estimate of the age of the females at their first pregnancy may be gained by examining the distribution of pregnancy among all the females of 80 in. and over. No pregnant seal less than 80 in. long has been found in Graham Land or in the Bay of Whales. Only females killed between February and May are included in the table below, since before February early pregnancies may perhaps have been overlooked. No females were taken between May and the following breeding season.

<i>Body length of females.</i>			<i>Pregnant.</i>		<i>Not pregnant.</i>		<i>Total.</i>
80–84 in.	1	25 per cent	3	75 per cent	4
85–89 in.	3	50 „	3	50 „	6
90–94 in.	8	100 „	0	0 „	8
95 in. and over	8	80 „	2	20 „	10
80 in. and over	20	71 „	8	29 „	28
85 in.	„	..	19	79 „	5	21 „	24
90 in.	„	..	16	89 „	2	11 „	18
95 in.	„	..	8	80 „	2	20 „	10

The data are of course not enough to make absolute conclusions possible. It is certainly clear that Crabeaters over 90 in. long are sexually mature, and only 11 per cent of them fail to be pregnant at any one time. Between 80 in. and 89 in., 40 per cent are pregnant, while if the subdivision is carried further, of seals in the 80–84 in. class, 25 per cent only are pregnant, and in the 85–89 in. class, 50 per cent. As already stated, Lindsey, in the Ross Sea, in March, found that 81 in. was probably the dividing line between the $\frac{1}{2}$ -year-old seals and those a year older, while in Graham Land the distinction was not so clear. These facts, combined with a consideration of the percentage figures of pregnancy, strongly suggest that though some of the young Crabeaters may become pregnant when a few months more than a year old, by no means all of them do so.

The Crabeater figures are not numerous enough to determine with any certainty possible differences in growth rate between the males and females in the first summer.

A greater amount of data would probably allow of the division of the year groups, by body length alone, to a rather greater age (as was possible for the Weddells up to about 20 months). Further division of the Crabeaters must then depend on other types of evidence.

SKULLS

(a) *Sex Differences*

There is no immediately obvious sexual difference between the skulls of the male and female Crabeaters. There are, however, certain tendencies, as set out below, which make it possible to sex most individual skulls with a fair degree of certainty. The degree of certainty attainable with the Crabeater skull is considerably greater than was the case with the Weddell.

(a) The male tends to develop the sagittal and lambdoid crests to a greater extent, though in the species as a whole this development is small. The sagittal crest is frequently double, particularly anteriorly in the early stages. The frontals are usually partly involved in the process in addition to the parietals.

(b) The skull length of the male tends to be greater in proportion to its breadth.

(c) The male skull tends to be a little heavier at the same length.

(d) The female skull tending to be a little broader in proportion results in the mandibular rami being set at a slightly greater angle to one another. The fusion of the rami in the female extends rather farther back, and a slight difference in their shape as well leads to the female having a more 'boat-shaped' mandible. The mandible of the female also tends to be more massive than that of the male.

(e) In the region of the fronto-maxillary junction and in the dorsal part of the cranium itself, the females tend to be more rounded, so giving the skull a more 'cylindrical' appearance. The skull of the male, being less rounded in this way and also tending to develop the crests to a greater extent, has something of a 'pagoda' appearance, with a tendency to show concave as well as convex surfaces on the dorsal part of the cranium.

In neither of his papers (on the Weddell and on the Crabeater seals) does Lindsey (1937, 1938) speak of any sexual differences in the skulls, and it is evident that he did not recognize any such.

(b) *Skull Dimensions and Proportions*

As has been done for the Weddell seal, here too for the Crabeater an attempt is made to determine the age classes from the appearance, size and proportions of the skull. Much of what has been written for the Weddell likewise applies in this case.

From his study of 32 Crabeater skulls from the Bay of Whales, Lindsey (1938, p. 460) provides the table reproduced below. It will be noticed that no sexual distinction is made.

Means of skull measurements for age groups, in mm.

			0.5 year.	1.5 years.	2.5 years and over.
Condyllo-premaxillary length	245	270	285
Zygomatic width	131	136	155
Mastoid width	142	146	154

In both the Weddell and the Crabeater, as the skull gets larger the zygomatic width tends to grow rather faster than the mastoid width. These year groups of

Lindsey's have been defined by him with the aid of the closure of sutures, etc., as well as the simple dimensions.

From Graham Land there are 37 skulls (19 males and 18 females) available for study. These skulls were taken over a number of months, while Lindsey's, like his body measurements, were limited to about one month. The lengths of the Graham Land skulls, like the body lengths, have been set out graphically month by month (fig. 34). A very marked break is at once obvious between a group of smaller

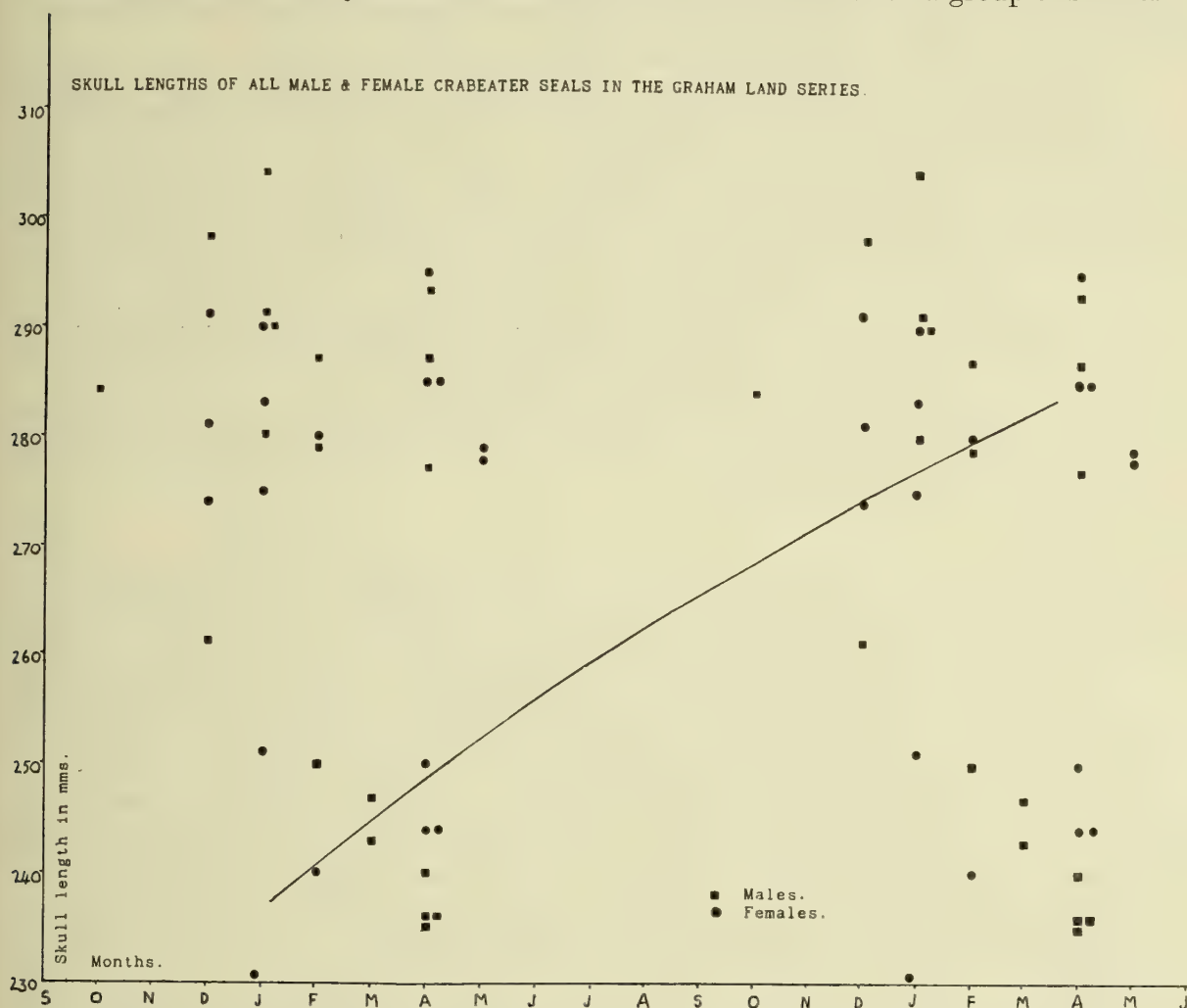


FIG. 34.—Diagram to show the lengths of the male and female Crabeater skulls in the Graham Land series repeated over the months of more than one year to show the most probable method of growth.

skulls and a group of larger ones. Between a length of 251 mm. (January) and 274 mm. (December) there is only a single skull (at 261 mm. in December). One cannot but conclude that here is a true separation of those seals a few months old from all those older. The anomalous skull (No. 87) at 261 mm. is from a 72-in. male which, it must be concluded, happened to possess an unusually large head. A female (No. 94) 6 in. longer than this anomalous male, has a skull length of 251 mm. Neglecting the one anomalous skull (which with little doubt belongs to the younger group), the

average skull length of the younger group is 242 mm. An average so calculated is of course devoid of any true biological significance, but may be compared with Lindsey's figure of 245 mm. for the average figure of his 0·5-year animals killed in March.

Beyond this separation of the first-season Crabeaters from those older, no further division into years is obvious from examination of the table of skull lengths of the Graham Land seals. As with the Weddell seal, there seems to be no well-marked regular change in proportions which might be of direct assistance in determining the age groups of the older seals.

A comparison of body lengths and skull lengths of individual seals shows (fig. 35) that they increase together in regular fashion, though there is a good deal more variation in this respect than in the Weddell. It is clear that males tend to have larger skulls than females of the same body length. Similarly, there is a greater variation among the Crabeaters in the connection of skull length and skull breadth (fig. 36) than there is in the Weddell, but there is no definite change in proportion between the two dimensions. The male Crabeaters tend to have a rather longer skull in proportion to breadth than the females, while in the Weddell the trend, if anything, is in the reverse direction. Again, in the Crabeater, skull length and skull weight increase roughly in proportion as they do in the Weddell, but the correlation is rather less precise (fig. 37). Exactly similar is the relation between skull length and face length in the two species (fig. 38).

(c) *Sutures*

As shown in the table above, Lindsey (1938) from his study of 32 Crabeater skulls from the Bay of Whales, separated three classes, 0·5 year, 1·5 years, and 2·5 years and over. He states (p. 460): "The skull of a Crabeater seal about 6 months old has the basioccipito-basisphenoid suture completely open. The frontal and parietal bones may be partly fused together. In the larger skulls of this first age group the parieto-squamosal sutures are completely closed. In the next group, consisting of individuals about 1·5 years old, the canines are larger, stronger, and have a more rugose surface. The inter-palatine sutures are still completely open, but the basioccipito-basisphenoid sutures have begun to close. The parieto-frontal suture is closed but not obliterated, and the parieto-squamosal is almost obliterated. At 2·5 years of age and older, the inter-palatine suture is nearly or completely closed. In the oldest skulls it is obliterated. The basioccipito-basisphenoid suture is obliterated medially in all the skulls of this third group, but may remain slightly open laterally in the 2·5-year seals. The inter-parietal suture is now completely closed, and the parieto-frontal and parieto-squamosal sutures are obliterated. It is significant that the progress of fusion of skull elements in each age group of Crabeaters parallels that in the Weddell seal. This indicates the validity of the above interpretation of age groups in the Crabeater seal, for which less material was available, and supports the conclusion that females produce young when 2 years old."

The present author is in general agreement with this statement of Lindsey's as to age distinctions based for the most part on sutural changes, but would suggest that the distinctions have been a little exaggerated. The division into three groups is less easy in the case of the females than in the males.

In the Graham Land seals of both sexes, the basioccipito-basisphenoid suture seems to close (except for its lateral extremities) in the change from the 0.5 to the 1.5 class, rather than in the 1.5 to 2.5 change as Lindsey found. Likewise the Graham Land seals seem to be rather more precocious in the closure of their fronto-parietal and parieto-squamosal sutures. The 1.5 to 2.5 years change in the males is clearly accompanied by the closure of the basisphenoid-presphenoid suture (a suture that in

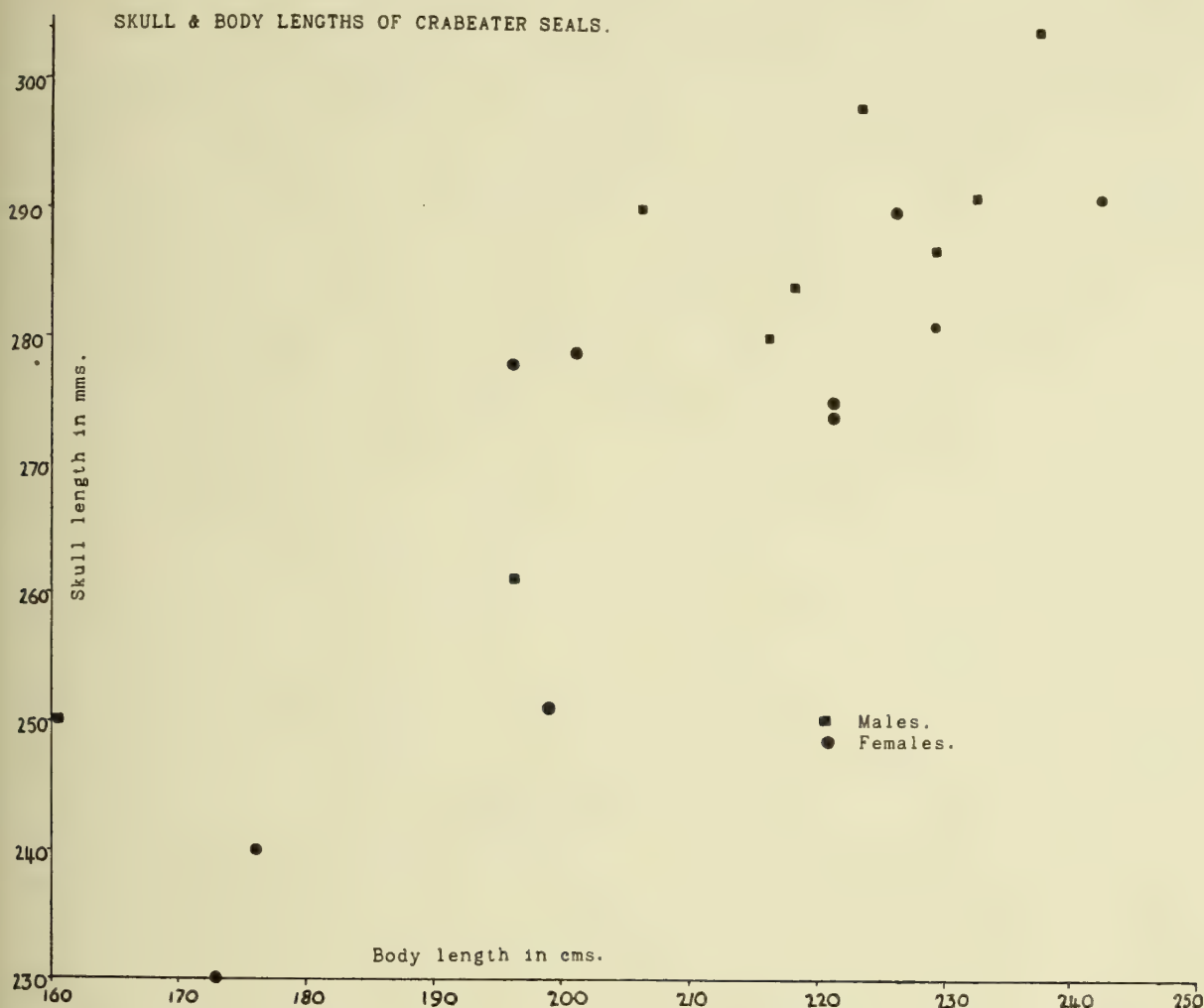


FIG. 35.—Diagram to show the relation between body and skull lengths of male and female Crabeaters in the Graham Land series.

the Weddell normally remains open throughout life). In the female seals from Graham Land there is only a poor distinction between the 1.5- and 2.5-year skulls. The 12 female '1.5-plus'-year skulls all have the basioccipito-basisphenoid suture closed, while 4 of them have the basisphenoid-presphenoid suture open. But of these 4, all but one at the same time have some degree of closure of the palate sutures (a combination not found in the male series). This suggests that in the female the state of the basisphenoid-presphenoid suture is not a sure criterion of age. It is possible that the precocity of the females that allows of a pregnancy during the second year

SKULL LENGTH & BREADTH OF CRABEATER SEALS.

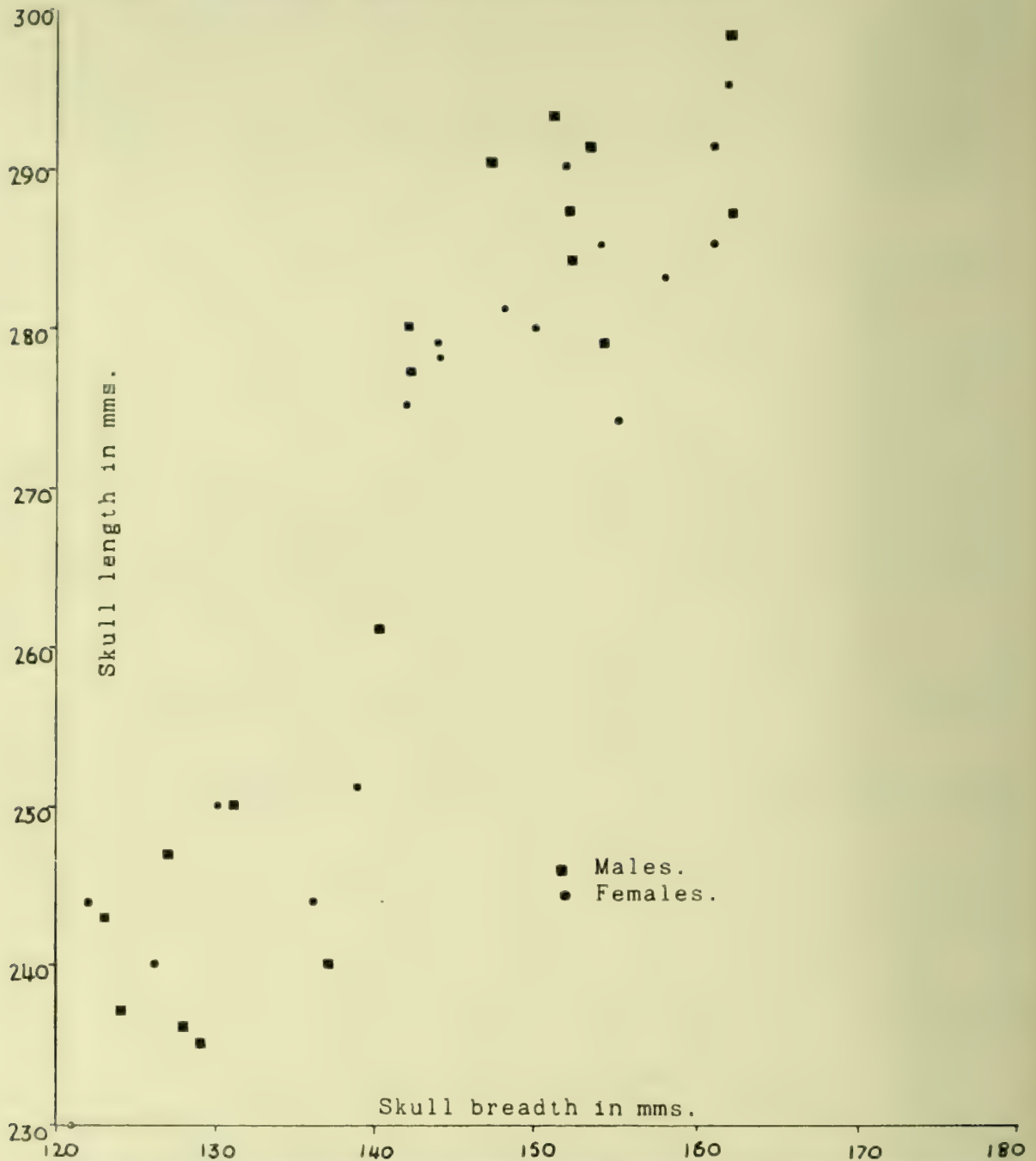


FIG. 36.—Diagram to show the relation between the skull length and skull breadth of male and female Crabeater seals in the Graham Land series.

is accompanied by a precocity of sutural closure, so making the distinction between the 1·5- and '2·5-plus' classes less certain than in the male.

As in the Weddell, the palate sutures appear to close gradually with advancing age, this taking place from before backwards. In no skull of either sex is the interpalatine suture completely obliterated. Two skulls of each sex (females 12 and 49,

males 92 and 93) have all sutures in front of the maxillo-palatine obliterated, but only No. 93 has this suture obliterated in addition. No. 93 alone also has the inter-palatine suture nearly obliterated, and this skull has been referred to previously as being the single instance in which serious breakage of the teeth has taken place.

LENGTHS & WEIGHTS OF CRABEATER SKULLS.

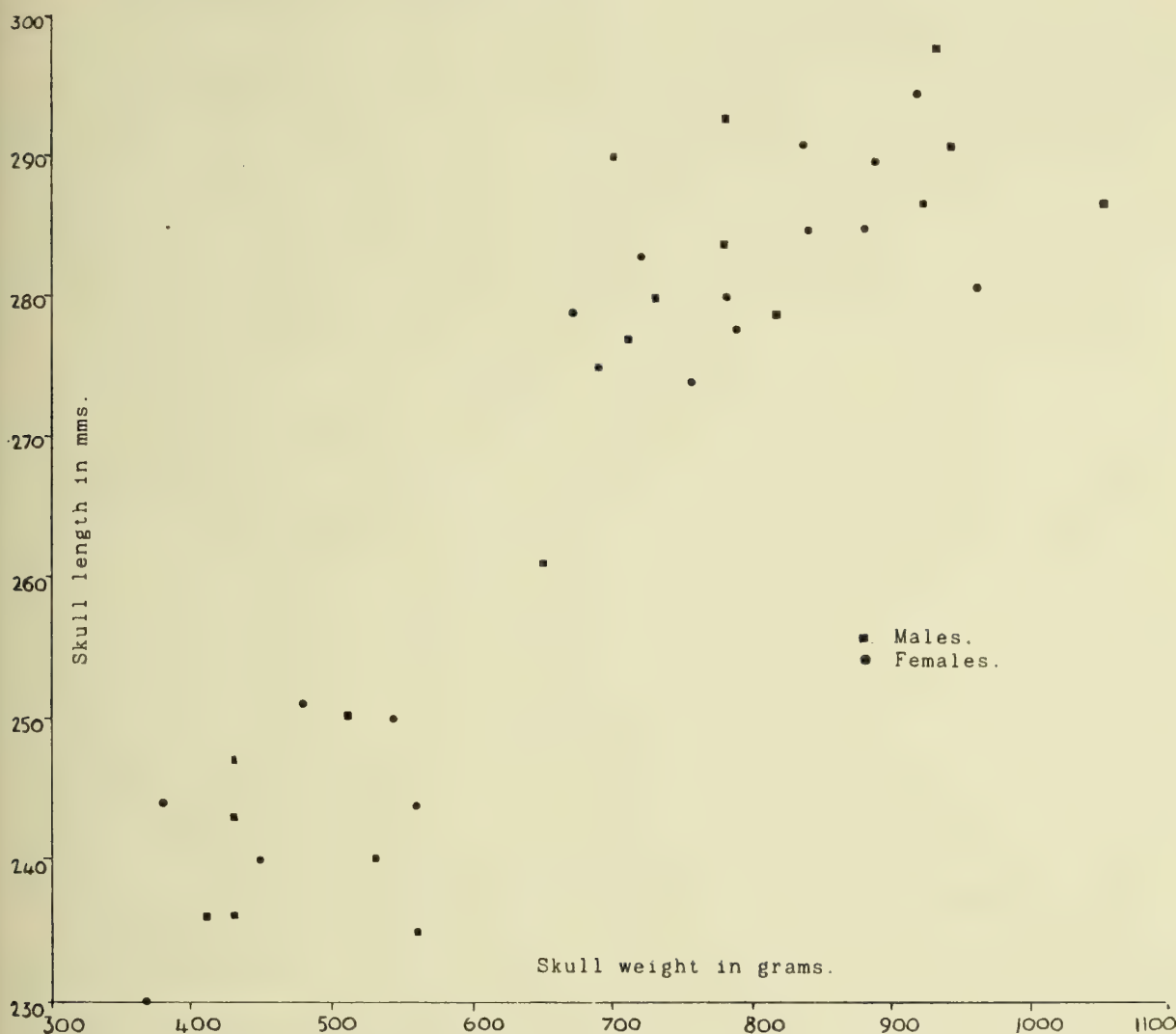


FIG. 37.—Diagram to show the relation between the skull length and skull weight of male and female Crabeaters in the Graham Land series.

Thus, from the study of body lengths and the skulls of series of Crabeater seals, it seems to be possible to distinguish $\frac{1}{2}$ -year-old seals from $1\frac{1}{2}$ -year-old animals fairly surely from the body lengths or the skull lengths, while the further distinction between $1\frac{1}{2}$ - and $2\frac{1}{2}$ -year-old animals can be made from the skulls, with sureness for the males, with less certainty for the females.

The precocity, which is so obvious a feature in the Crabeater seal, compared with many of the Pinnipedia, is a telescoping of the young stages into a shorter period

CRABEATER SKULL & FACE LENGTHS.

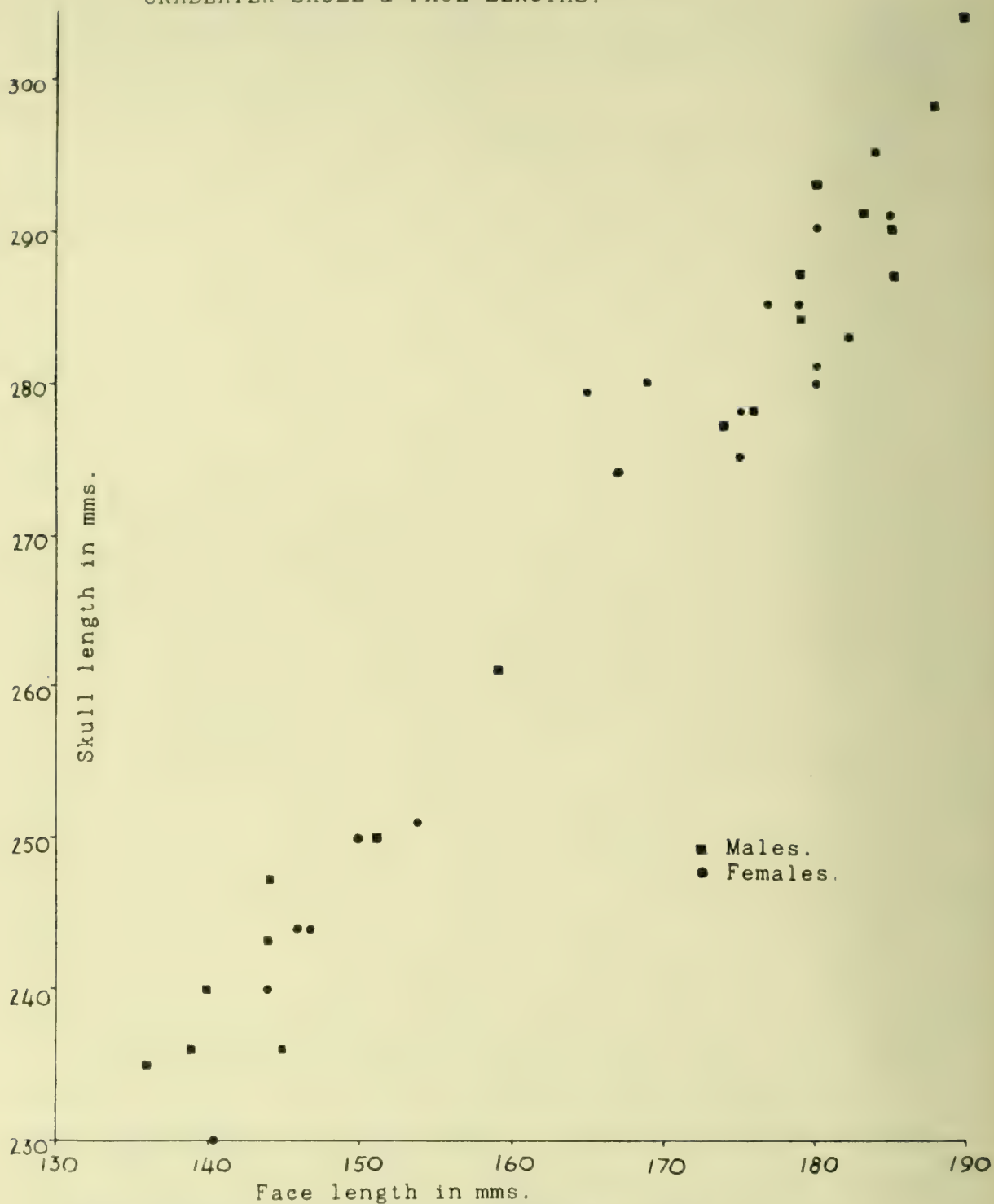


FIG. 38.—Diagram to show the relation between the skull length and the face length of male and female Crabeater seals in the Graham Land series. The 'face' length is the distance between the front border of the premaxillae and the suture between the basi- and pre-sphenoid.

of time. The result of this telescoping is clearly the earlier acquirement of the adult characters, and for this reason alone one might expect to find a greater difficulty in distinguishing the year groups, for a greater proportion of the whole population will be 'adult', and the individual can be classed as 'young' for a proportionately shorter time.

OVARIES

An attempt has been made to use the ovaries of the Crabeater seals in exactly the same way as has been done for the Weddell, and the same method of reasoning may be used for the two species. But the data for the Crabeater are very considerably fewer, there being only 25 pairs of ovaries instead of the 65 pairs from the Weddell, so that conclusions in some directions are not possible. The most unfortunate circumstance is that, for reasons already explained, of the 25 pairs of Crabeater ovaries in only 5 instances is the skull of the same individual available as well. This deficiency sadly curtails the value of the ovarian examination. Attempts to correlate number of corpora lutea with the appearance and dimensions of the skulls are thus possible only to an extremely limited degree.

The Crabeaters, like the Weddells, behave synchronously. At any one date all the foetuses tend to be of roughly the same size, though there would seem to be a little more variation than is found in the Weddell. All the Crabeaters pup at about the same time (September), and all must copulate at about the same time (December). As in the Weddell, again, when the ovaries are examined, it is found that the corpus luteum of pregnancy is of large size throughout at least the first half of gestation (no material is available for the second half), and persists for long after parturition. No pair of Crabeater ovaries has been examined that contained more than a total of 6 old corpora, including that of an existing pregnancy. Whether the female Crabeater is truly monoestrous, being capable of shedding but one ripe ovum in each sexual season, or is polyoestrous but usually becomes pregnant at the first ovulation, cannot yet be stated with certainty, just as no absolute conclusion has been possible for the Weddell. Whether the old corpora lutea persist throughout life (as there is strong presumption that they do in the Weddell) or disappear completely at an earlier date, cannot be determined with certainty on the material available, but the former alternative is probably correct. There is no direct observational difference between the ovaries of the two species: whole ovaries or sections of them are not distinguishable by any external or internal macroscopic appearance or condition. Neither in the Crabeater nor in the Weddell seal is there any evidence to show whether ovulation is spontaneous or is dependent on copulation.

Sexually mature female Crabeaters become pregnant every year, though perhaps 20 per cent of them may fail to do so. This proportion of 'missed' pregnancies is slightly higher than the proportion found in the Weddell seal. It is quite clear that the Crabeater cannot both be actively polyoestrous and have completely persistent corpora lutea, yet no female shows a total of more than 6 corpora. It is presumably possible that the regression of a corpus luteum associated with an unsuccessful ovulation might be more complete, so that it disappeared absolutely, while the corpus luteum of pregnancy persisted through life; but no such case seems to have

been demonstrated. In the Weddell the simultaneity of pupping and therefore of copulation, and the frequency distribution of persisting corpora lutea, were used together to support the very strong presumption that normally a single ripe ovum is shed each year and that each corpus persists throughout the life of the animal. In the Crabeater there is almost, but not quite, the same simultaneity of copulation (to judge from the foetal sizes), and the smaller number of ovaries available makes it difficult to draw conclusions from the frequency distribution of the numbers of corpora lutea. The frequency distribution curve of corpora (fig. 39) is, however, of the same general shape as that of the Weddell, rather than resembling either of the theoretical

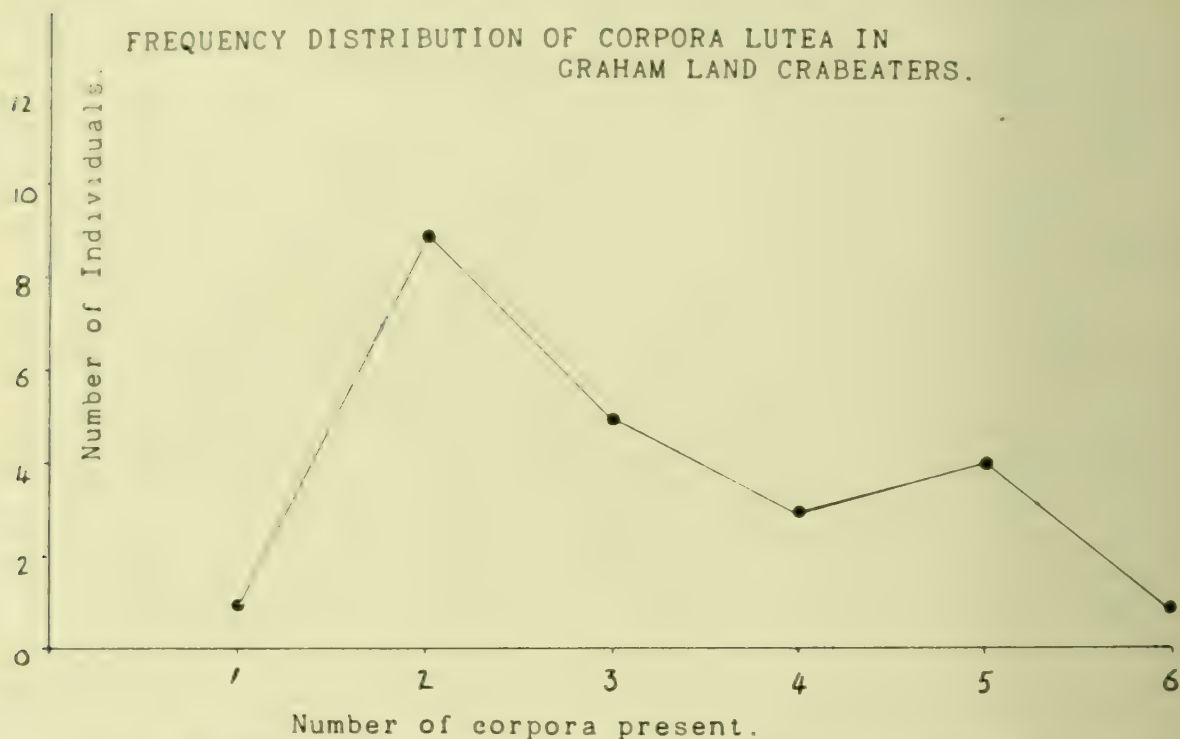


FIG. 39.—Diagram to show the frequency distribution of numbers of corpora lutea in the ovaries of Graham Land Crabeater seals.

curves (fig. 19) based on the non-persistence of the corpora lutea. The deficiency in the amount of data is clear, but it seems probable that the corpora resemble those of the Weddell in persisting as long as the animal usually lives.

The distribution of the numbers of corpora lutea in relation to the body lengths of the individual seals is inconclusive (fig. 40), but there is nothing out of accord with the view that increase in number of corpora runs parallel with increase in body length. Clearly they must do so to some extent since both are necessarily dependent upon time (age), and there would be some parallelism even though the corpora do not survive as long as the individual. But, as stated above, though the material is rather small in amount, there is every appearance of the Crabeater resembling the Weddell in the persistence of corpora lutea throughout life. The actual coefficient of correlation between number of corpora lutea and body length in the Crabeater seal is 0.46 for 24 pairs of observations. This figure is 'significant' (it would only occur by

chance in between 1 per cent and 5 per cent of cases) whereas the figure for the Weddell is 'highly significant' (being likely to occur by chance in less than 1 per cent of cases).

It will be seen in the diagram of frequency distribution of corpora lutea in the Crabeater (fig. 39) that the number of animals possessing a single corpus luteum in the ovaries is extremely small compared with the number that possess two corpora (i.e. 1 seal compared with 9 seals). A similar occurrence, though not so marked, was noticed among the Weddells. There, a very natural explanation of it at once presented itself. It was evident that the young animals, pregnant for the first time, had not yet acquired completely the adult lying out habits (at which time only could the animals be killed), and so were appearing in the ovarian collection in less than their true proportion. Were the data more extensive, the same or some similar explanation might be found for the Crabeaters, but at present it is not apparent. There is a possibility that should be mentioned, namely, that the virgin seals, or some of them, have not become perfectly synchronized with the normal breeding cycle of the species. Possibly virgin seals might ovulate for the first time in their lives very early on in the season, at a time before the bulls were ready to impregnate them, and thus it would come to be the virgin's second ovulation that gives rise to the first pregnancy. Since the Crabeaters are killed in the summer shortly after the mating season is over, the seals pregnant for the first time would, on this hypothesis, already possess two corpora lutea, one the regressed product of the unsuccessful first ovulation, the other the functional one of pregnancy. The slightly greater variation in foetal sizes in this species than is found in the Weddell suggests that the synchronization of the breeding cycle is rather less perfect. Such an hypothesis, or the alternative one that the young seals have not yet acquired the adult lying out habits, must remain entirely speculative until such time as more abundant data are available.

It is perhaps surprising that no female Crabeater was found to possess a total of more than 6 corpora lutea in the ovaries. In the Weddell, however, where so many more ovaries are available, the proportion with more than this number is very small, so that the non-occurrence of any number over 6 in the Crabeater is probably due to chance.

In conclusion, it appears probable that the Crabeater resembles the Weddell in producing a single ripe ovum in each sexual season. The mature females normally (i.e. 80 per cent of them) become pregnant every year, and the corpora lutea persist throughout the life of the individual. As already emphasized from time to time, however, the ovarian data are inadequate to make this conclusion absolutely certain.

CORRELATIONS AND AGE DETERMINATION

It has already been pointed out that precocity represents a telescoping of development into a shorter period of time, and that this period occurs when the animal is young. It follows that the individual spends a greater proportion of its whole life in the 'adult' condition, and that at any given time a greater proportion of the population will be in this condition, compared with a species where there is not the same precocity of development. In a 'non-precocious' species, the changes (morphological and dimensional) between the new-born condition and that of old

age are spread out more or less evenly over a considerable period of years. In the 'precocious' species these changes are spread over a rather short period of years. In the 'non-precocious' species it will probably be possible to distinguish the age groups with fair accuracy (on general morphological grounds) for a considerable period of years, perhaps throughout life. In the 'precocious' species such distinction can probably only be made during the first few years of life, and the more precocious the species in attaining the adult condition the smaller will be this number of years. Precocity itself must be considered a recent modification in the group of mammals concerned (rather than being considered the primitive condition in mammals) and

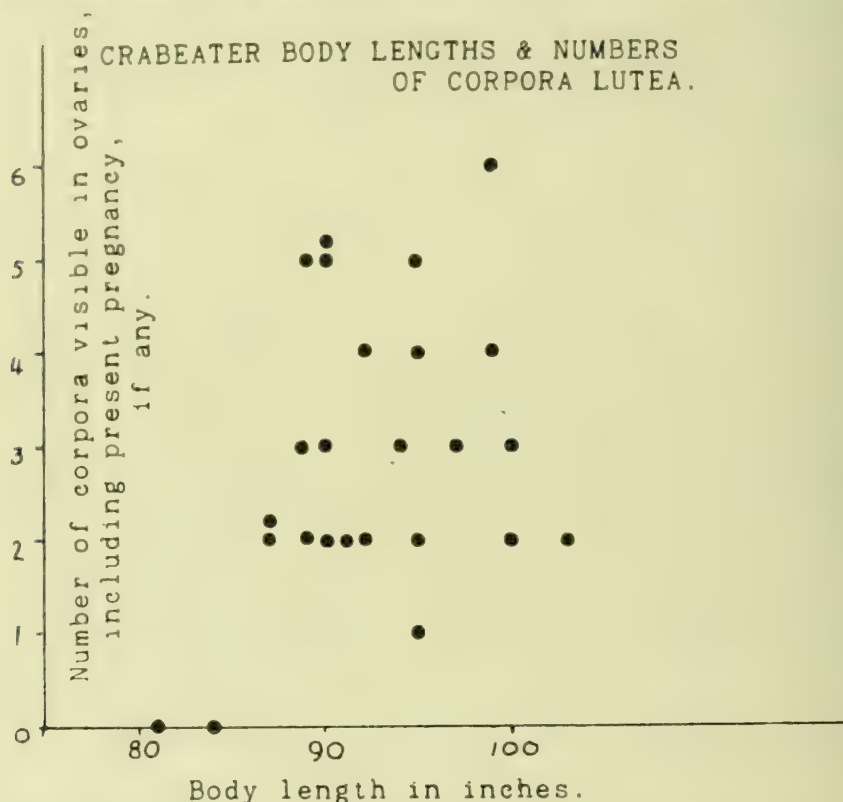


FIG. 40.—Diagram to show the relation between body length and the number of corpora lutea in the ovaries of the Crabeater seals in the Graham Land series.

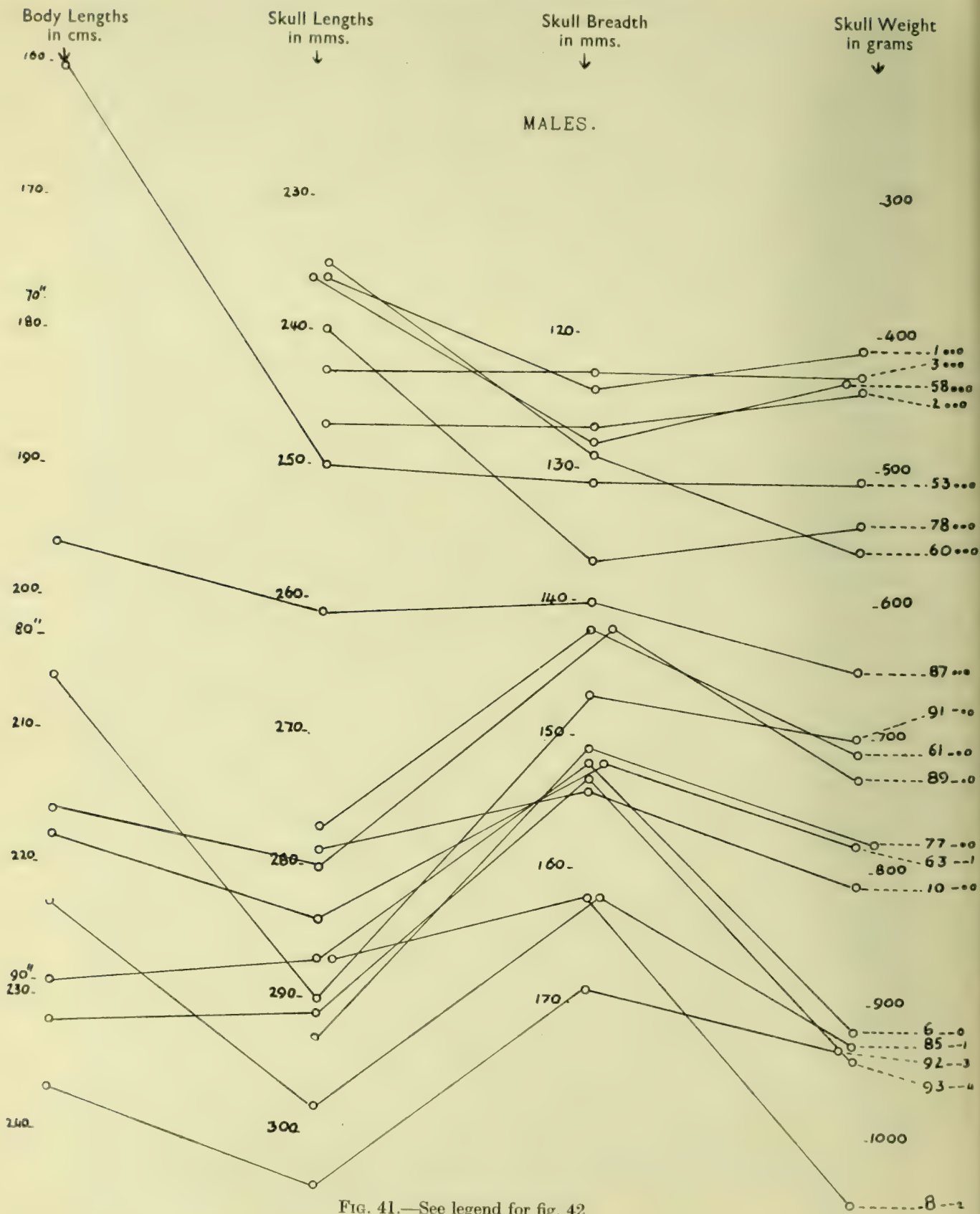
therefore it is probable that variations will be found in its amount and effects. That is to say the relative precocity of different morphological features (for example, the relative times of closure of certain sutures in the skull, and the attainment of a certain size) may not yet be absolutely fixed.

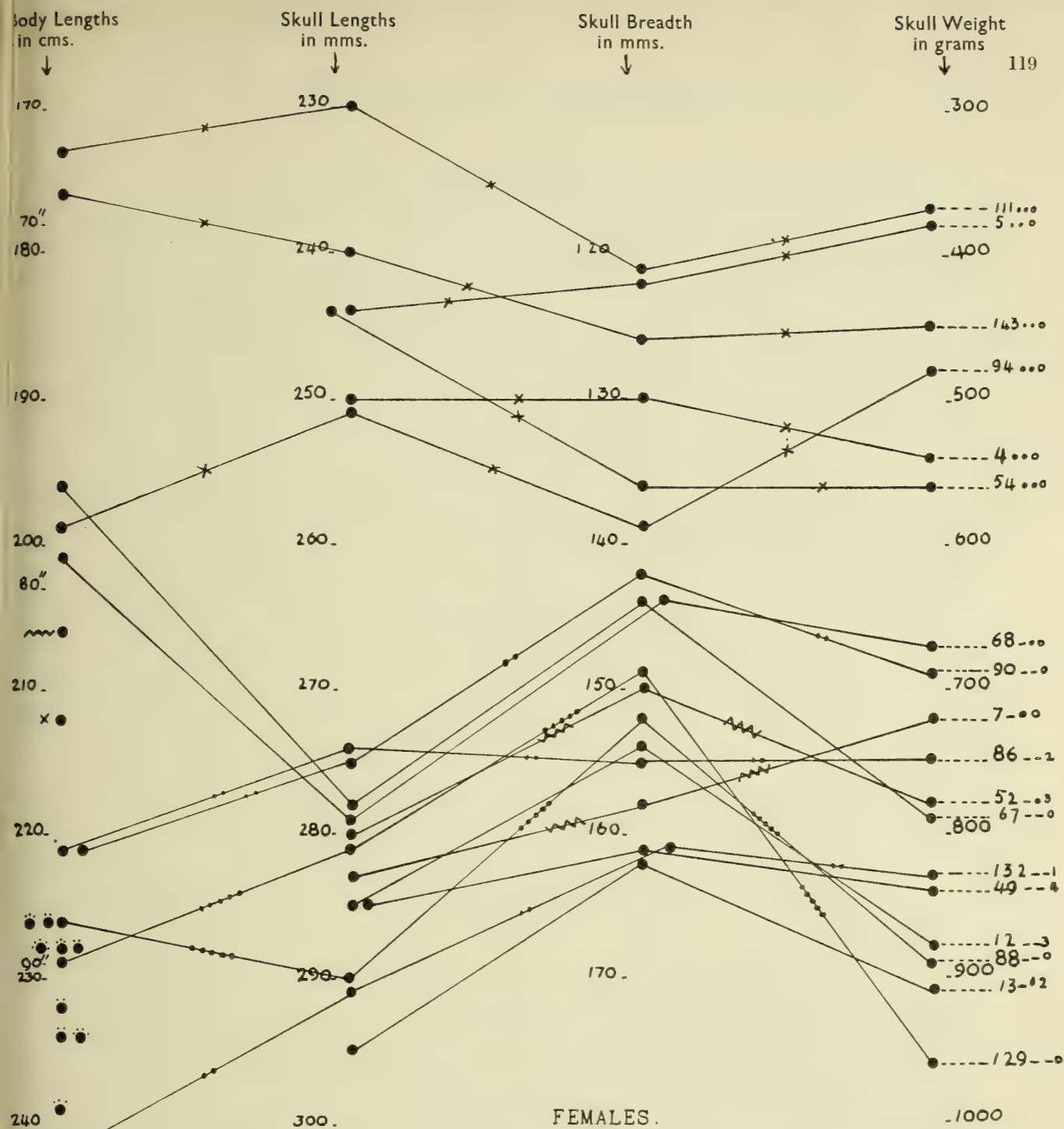
So far as present knowledge goes the True seals are all precocious compared with the Eared seals (Osgood, Preble, and Parker, 1914; Hamilton, 1934, 1939). For a precocious species like the Weddell seal, it has been shown in the earlier part of this paper that though the younger groups may be distinguished on morphological and dimensional grounds with fair certainty up to the age of about 40 months, the distinction cannot be carried further. Compared with the Weddell seal, the Crabeater has now been shown to be still more precocious, some of the females breeding a full year earlier than the young Weddells; that is to say, they

become sexually mature in only a little more than half the time taken by the other species (namely at 15 months instead of at 27 months). The change in form and dimensions from the juvenile to the full-grown condition is correspondingly compressed into a shorter period of time. Hence, in the Crabeater, on these grounds, certain distinction between age groups is only likely to be possible for a still smaller number of years than in the Weddell. This is not to imply that sexual and physical maturity are necessarily coincident, but clearly in mammals there must be some interdependence, and there is the strong probability that the individuals of a species which early becomes sexually mature will tend to acquire the mature physical characteristics at a correspondingly earlier age. A more absolute measure of age, such as the ovaries are believed to provide, may, however, enable the older individuals to be aged with reasonable accuracy.

The extent of the possible separation into age groups on the criteria of body measurements, skull dimensions and sutural closure have already been considered separately. Now they may be considered in conjunction, so far as that is possible on the evidence, together with the ovarian data available. The composite diagrams (figs. 41, 42) are self-explanatory. The body length, skull length, breadth and weight, the number of corpora lutea in the ovaries, and the degree of closure of certain sutures are all shown so far as known. In both sexes the division between $\frac{1}{2}$ -year-old seals and those a year and more older is very obvious. The group of male seals at $1\frac{1}{2}$ years old as distinguished by the basisphenoid-presphenoid suture remaining open while the parieto-frontal, the parieto-squamosal and the basioccipital-basisphenoid sutures have closed, exactly corresponds with a group distinguished fairly clearly by skull weight (with the exception of Skull No. 63, which is evidently of greater age). Among the females, however, this separation of the $1\frac{1}{2}$ -year-old animals from their seniors is by no means so clear. Three females still have the basisphenoid-presphenoid suture open while the palate sutures are already partly closed. The diagram also demonstrates that among the female Crabeaters the relative dimensions are much more variable (i.e. from the diagrammatic point of view the connecting lines cross more frequently and at less acute angles than among the males). It is clear, in fact, that the '1½-years plus' females cannot be further divided into groups with any certainty unless one feature is held to be a far better diagnostic of age than any other. The only character that could fairly be used in this way is believed to be the number of corpora lutea in the ovaries. The amount of ovarian data is small, but if the ovarian hypothesis be accepted, it is evident that animals of the same (ovarian) age may vary considerably in their skull and body dimensions (as was found, though to a rather lesser extent, among the female Weddells). It may well be, though of this there is at present no direct evidence, that those female Crabeaters which become pregnant when 15 months old subsequently grow more slowly, or cease to grow at an earlier age, than those which did not. That is to say, the sexually precocious females may have already more nearly reached physical maturity.

It thus becomes clear that Crabeater seals cannot with any certainty at present be divided beyond separating the males, into $\frac{1}{2}$, $1\frac{1}{2}$, and '2½ plus' year groups (Plates VIIa, VIII), and the females into $\frac{1}{2}$ and '1½ plus' groups. The difficulty in defining the year groups is probably a direct result of the precocity of development found in the species.





FIGS. 41 and 42.—Composite diagrams to illustrate the possible dimensional basis of year groups of male and female Crabeater seals in the Graham Land series. All the sexed skulls in the series are included. The majority of these were taken in the 'summer' months (late October and early May being the extreme limits), so that the seals represented must have been within a few months of being of the same age, or separated approximately (though not exactly as in the case of the Weddells) by a precise number of years. Lines join the reference marks belonging to each individual. The serial number of each skull is inserted at the right. The symbols •, ••, etc., indicate the number of corpora lutea in the ovaries, and where these are not available the symbols * and — are used where it is known that the animal was 'not pregnant' or 'pregnant' respectively. Further symbols (three in number) inserted to the right adjacent to the serial numbers of the skulls, refer to the closure of certain sutures. The first (• open, — closed) refers to the Pa/Fr, BSph/BOcc and Pa/Sq sutures which close approximately at the same time. The second symbol refers to the closure of the BSph/PSph in the same way. The third symbol (0, 1, 2, 3, or 4) refers to the degree of closure of the palate sutures treated as a whole. In fig. 42 are inserted a number of further females whose body lengths are known and whose ovaries have been examined, but whose skulls are not available.

THE COMPOSITION OF THE CRABEATER POPULATION

Now that the series of Crabeater skulls has been split up as far as possible on the evidence, it is at once apparent that the older seals are fewer in number than would have been expected. In the males, where the year divisions are more precise, there would appear to be in the Graham Land series 7 skulls of $\frac{1}{2}$ -year-old animals, probably 6 of $1\frac{1}{2}$ -year-olds and 6 of '2 $\frac{1}{2}$ plus' years. Among the females there are 6 evidently $\frac{1}{2}$ -year-old and 12 '1 $\frac{1}{2}$ -plus'-year skulls (of which 12, 3 are believed to have been pregnant for the third time, and 2 pregnant for the fifth time). The complete set of figures of body-lengths of Crabeater seals may now be compared with the length column in the diagrams (figs. 41, 42) used above, so as to increase the amount of data on which conclusions as to the composition of the population may be based. It then seems that the proportion of the total population that is made up of the older seals is smaller than is reasonably possible. Though it has not been possible to distinguish the year groups of either sex beyond a rather early age, enough is clear to show, approximately, which may be called 'older' seals. A body length of 220 cm. (c. 87 in.) seems from the diagram to be a reasonable datum line to take. Seals of both sexes having a body length of less than 220 cm. are probably $1\frac{1}{2}$ -years-old or less, those longer than 220 cm. are probably more than $1\frac{1}{2}$ years old. This latter group may be termed the 'older' seals. Of the total number of Crab eaters measured 52 per cent of the males and 42 per cent of the females are, on these grounds, to be termed 'older' seals. But it is quite clear that in the Crabeater population, where at most a single pup can be produced by each mature female each year, even if they do begin to breed at a little more than a year old, considerably more than half the total population must consist of 'older' animals. Since in fact only 52 per cent of the males and 42 per cent of the females are found to belong to the older group, it follows that the Crab eaters represented in the data cannot be a true sample of the population as a whole.

That he was dealing with a disproportionately large number of young animals was quite clear to Lindsey (1938) in the Bay of Whales. Of 61 individuals measured by him 42 were less than a year old. In Graham Land, however, the fact that the Crab eaters taken were not representative of the whole population was not obvious until the complete analysis of the data had been made. It now becomes apparent that the inshore migration of Crab eaters in Graham Land, in being made up of an excessive number of young animals, more nearly resembles the Ross Sea migration, though the proportion of older animals is considerably greater than in that area. This being so it cannot confidently be assumed that the 'older' females that do take part in the migration are a representative sample of the whole 'older' female population. This fact, together with the inadequacy of the data available, at present removes further study and analysis of the composition of the Crabeater population beyond the realms of legitimate speculation.

THE COMPARATIVE BEHAVIOUR OF THE PINNIPEDIA

Among the seals a number of phenomena, polygyny, prolonged gestation, precocity, etc., seem to be intimately connected one with another, but as yet it is scarcely possible to determine with any certainty which of the various factors are causative and which resultant. An attempt is here made, however, to unravel some of the main points. In an addendum is set out in condensed form the present knowledge of the essential points in the life histories of all species of Pinnipedia.

The seals of all three groups (*Otariidae*, *Odobenidae*, and *Phocidae*) differ from the *Fissipedia* in the much longer period of gestation (from 9 months to a year), instead of, for example, 15 weeks in the Tiger, and 6 months in Bears (Peacock, 1933). The seals also differ from the *Fissipedia* in the absence of multiparity (apart from rare cases of twinning), and the much more advanced stage of development at which the pup is born. This long period of gestation, among the Phocids, is followed by an extremely short period of lactation. The minimum lactation period is a few days (Crabeater unproven), but more usually it lasts only from 3 to 6 weeks. In the Walrus on the other hand, lactation lasts for not less than $1\frac{1}{2}$ years (Chapsky, 1936). In some of the Eared seals (e.g. Southern Sea Lion, Hamilton, 1934), the female and pup may keep company even for a year. The single seal pup at birth, in proportion to the total weight of the mother, is greater than the combined weight of the litter of any *Fissiped*. A pup of great size at birth is presumably more easily carried by an aquatic animal where the maternal body has not to be supported clear of the ground. An extension of this truth is perhaps seen in the fact that the pups of the (less aquatically-adapted) Eared seals are rather less in proportion to the mother at birth than is usual among the True seals. When, however, the pregnant female Phocid near full term emerges from the water on to the land or ice and moves over it in 'looper-caterpillar' style, it is remarkable that such laboured movement on the belly does not have serious consequences. Possibly the possession of a zonary placenta (12 in. wide at full term in the Weddell) adds to the stability and safety of the foetus at such times.

From the teleological point of view it is clearly to the advantage of an animal living in an aquatic medium, where parental care is presumably more difficult than on land, to prolong the gestation period, so that the young may be in a more advanced state at birth. Among the Whalebone whales, where a secondary feeding apparatus is to be developed before independence of the young can be attained, lactation is necessarily somewhat prolonged (often to 6 months or more, Mackintosh & Wheeler, 1929, *et al.*). In the True seals, however, where the adult feeds with the original tooth mechanism, it has been possible (again to speak teleologically) for compression and acceleration to take place, so that the young may be born with the adult mechanism almost complete. Thus in the Weddell and Crabeater seals the milk dentition reaches its maximum size at about one-third of the way through pregnancy, after which it is reabsorbed and the young are born with the adult teeth already projecting from the gums. Lindsey (1937) has shown for the Weddell seal that on the average the adult dentition is completely attained by the age of 34 days. There is clearly a connection between shortness of lactation and the precocity of the

permanent dentition, but which is the forerunner of the other is purely surmise. In the Eared seals the milk dentition though greatly reduced and never functional, is still present and projects from the gums at the time of birth.

In addition to the dentition and the shortness of lactation, the True seals also tend to be precocious, relative to the Eared seals in a number of other characters, though there is variation in its extent between the different species. One of these is the condition of the coat at birth. The typical state is for the pup to possess a thick woolly coat at birth, quite different in appearance and texture from the straight hair coat that is attained later. The young of most species of True seals moult this natal coat at a few weeks of age, just prior to the time at which they enter the water, though in exceptional circumstances the pup is capable of starting its aquatic existence even before this has happened. The infantile woolly coat of the Harp or Greenland seal forms the 'white coat' of the northern fisheries. In a few species, however (Hooded, Nansen, 1925, and Common seal, Havinga, 1933), the woolly coat is moulted just before birth and the fallen hairs are shed with the placenta and foetal membranes, and the pup is born in a juvenile coat of adult type.

The age at sexual maturity among seals is variable, but the True seals as a whole seem to be precocious in this respect compared with the Eared seals. This is much more marked among the males than among the females. The greater age at which the males become sexually mature in certain species is clearly connected with the sexual disparity in size and polygynous habits. Distinction should be made, however, in such cases between actual sexual maturity (i.e. the age at which ripe sperm is first present in large amounts) and functional sexual maturity (i.e. the age at which the bulls first get the opportunity to exert their sexual powers). In the present state of knowledge of the polygynous species, the age at which the bulls first possess sperm seems to be unknown. It would appear that the True seals most frequently become sexually mature in about the third year in both sexes. In the Eared seals the females are usually a year later, while the males do not get the opportunity to exert their sexual power until about the sixth year. The ages at which sexual maturity is reached in the various species of seals, so far as they are known, are set out in an Addendum which summarizes the life histories (Addendum I).

Further points now to be considered are polygyny, the simultaneity of pupping, and the length of gestation, points which are much interwoven in their cause and significance, together with the fact of copulation being possible on land and/or in the water. The point of origin of the present line of thought is that no seals are yet so perfectly adapted to the aquatic environment that they have been able to dispense with the land entirely. All pregnant female seals must leave the water to pup. The nearest approach to actual breeding in the water is found in the Crabeater and Common seals, the pups of which are stated to enter the water naturally at most within a day or two of birth. The pup of the Common seal indeed, frequently must swim at the first flood tide after its birth on a sandbank (Millais, 1906).

Most mammals have a definite season in the year when breeding takes place, the precise season being fixed by the factors which control the ripening of the ovarian follicles, and the necessity for the young to be produced at a suitable season of the year. Seals of all species follow this habit, the young being born within a well-defined short period. The time of pupping is the spring and summer in both

the northern and southern hemispheres for all species except the Atlantic or Grey seal which, in most parts of its range, breeds in the northern autumn. The Grey seals of the Baltic apparently are spring breeders (Hjort & Knipowitsch, 1907). The autumn breeding time of this species seems singularly ill-adapted to the needs of the pups, many of which are drowned each year by the heavy seas beating up on to the skerries and small islands where they are born. Those Grey seals, as on the Cornish coast, which prefer to breed in deep caves, are presumably more free from this danger than their fellows of the Hebrides and elsewhere. The Grey seal is also peculiar in that the variation in the time of its pupping is greater than in almost all other species. Even within a small population of say, 100 females, there may be as much as 3 months difference in pupping time, and the peak period within those 3 months is not well marked. Most species of seals have a pupping time whose period is rather more than 6 weeks, and within which there is a definite peak period when most of the births take place. One or two species, in particular the Harp seal, have a pupping time that is almost confined to a few days, whose dates are the same from year to year in any one area (Nansen, 1925; Colman, 1937, *et al.*).

Since the members of a species of seal tend to breed at the same time, it follows that at this period there must be some degree of crowding, for the seals that were previously spread over an area of ocean or inshore water, must now come to a coast or on to ice. Apart from this purely 'topographical' necessity for crowding at the breeding season, most species of seals are definitely gregarious, collecting together to pup even when there is ample space on the beaches or on the ice. Thus the Harp seals collect in vast concentrations to pup, all the seals of the species in the North Atlantic region doing so in one of the three recognized areas (off Newfoundland, in the White Sea, or in the 'West Ice' (Colman, 1937, *et al.*)). Well-defined pupping grounds are, in fact, characteristic of almost all species of seals. The concentration of seals at the pupping time reaches its climax among these highly gregarious Harp seals breeding on the ice, in the Elephant seals of the subantarctic islands (in particular S. Georgia at the present day), and in the Fur seals of the Pribilof Islands.

So far the breeding seals have been considered simply from the female point of view, arising from the gregarious habit, the simultaneity of pupping, and the necessity for doing so on land or ice. Now the habits and capabilities of the males must be superimposed, as it were, on these female characteristics if a true picture of the breeding complex is to be obtained. The males of many species of mammals possess ripe sperm throughout the year, and this seems usually to be the case with the land Carnivora, but it is not necessarily so with the Pinnipedia. It can well be imagined that a great concentration of female seals at the pupping time will inevitably provoke the males to a state of great sexual excitement and activity. Whether actual copulation will occur soon after the birth of the pups will then depend upon the state of activity of the ovaries, and whether the individual female will accept the male. A period of heat shortly after parturition is common to many mammals. At least in the Weddell and Crabeater seals it seems to be normal for the ovaries to alternate in their activity, and for the ripe ovum to be shed from the opposite ovary from that containing the corpus luteum lately functional in the last pregnancy. This is not invariable but seems to be the normal sequence. The Walrus, breeding in alternate years, is the only species definitely known not to pup in each

year once sexual maturity of the female has been attained. (Chapsky, 1936.) The Bearded seal (Chapsky and Kovolev, 1938) frequently misses a season between successive pregnancies.

Whether or not the actual concentration of breeding females and the co-presence of wandering males was originally and is now itself a factor in bringing the females to the pitch of renewed ovulation is unknown but by no means impossible. Fraser Darling's (1938) suggestion as to the beneficial effects of concentration in the breeding of colonial birds may well have parallels among the seals at the pupping time. Whatever the stimulus to renewed ovulation, if it does occur within a few weeks of parturition, and copulation follows, it comes about that gestation must be these few weeks less than a year, if the annual pupping date is to remain unchanged. Among seals where the pup is of such great proportionate size, the 'strain' (to use the word in a popular but ill-defined sense) of pregnancy must be great, and from this point of view it would appear peculiar that a new pregnancy is initiated so swiftly after the termination of the last. Further, in the Eared seals and in the Elephant seal, there is a period of several months when the females are both pregnant and lactating. It may be significant in this connection that in various species of seals, for example in the Weddell and Crabeater, the growth of the embryo in its early stages appears to be slow. There is some evidence of a definite period of quiescence in several other species between the observed mating time, when fertilization presumably occurs, and the start of active embryonic growth and development (e.g. Hooded seal, Høst, private communication; Harp seal, Nansen, 1925; Bearded seal, Chapsky and Kovolev, 1938). There would appear here to be a very nice adjustment of developmental velocities to allow of the pups being born on almost precisely the same date each year.

In the mouse ovulation takes place a day after parturition, and the same circumstance is known in a number of other mammals. In seals, however, there is no certain case of parturition and copulation taking place at a less interval from one another than about 10 days. Therefore if the females of a species of seal are to pup at the same date each year, the period of gestation cannot be greater than 355 days. Hamilton (1934, p. 300), speaking of the Southern Sea Lion, states: "Pairing takes place soon after the birth of the pup. . . . There is . . . a space of 8 days between the latest live birth and the latest impregnation, so that the period of gestation must be a few days under a year." Consider now the effect should the parturition-copulation period and gestation together exceed a year. It is now no longer possible for any one female to pup at the same date as she did in the previous year. If the parturition-copulation period plus gestation only exceeds the year by a small amount there will be a tendency for the individual female seal to pup a few days later in each succeeding season, so spreading the pupping of the species over a rather longer period. Examples of this phenomenon must then be looked for among those species whose pupping seasons, although limited, yet are spread over several weeks or even one or two months. The case of the Elephant seal is the best attested. Matthews (1929, p. 236) remarks: "The pups are born from the last week of August to the end of September and some even in October, so that the season lasts for 6 weeks or more. Most of the late pups are first ones, their mothers having been impregnated for the first time late in the last season. The virgin cows haul out much later than the others

and join the harems already on the beaches. . . . The cow will not take the bull until a week or 10 days after the birth of the pup." More recent extended personal observation by Roberts (private communication) suggests, however, that Matthews is partly incorrect in his statements, or chanced upon abnormal individuals. The breeding time is more extensive than Matthews relates and is scarcely well started before the middle of September, and newly-born pups are not rare even in December, and a few have been found as late as early January. Matthews' statement that "the late pups are *first ones* their mothers having been impregnated late in the last season" can scarcely have solid grounds in proof (in the absence of ovarian examination and/or series of measurements of body length). Rather would it appear that the smallest females tend to have the earlier pups, the larger (and older) animals pupping somewhat later. The December pups are regularly found to be those of very large females. There is little doubt that what is happening is that gestation plus the parturition-copulation period totals rather more than a year. As the female advances in age her pupping date is consequently retarded season by season by the difference between 365 days and the sum of her gestation and parturition-copulation periods. In the present state of our knowledge it is not possible to say what this difference is as an exact number of days, but it is probably not great. The difference in time between the earliest and latest pups is still scarcely more than 3 months and the average female is not likely to pup less than 5 times in her life.

Such a gradual spread in the pupping time, however, can probably not go on indefinitely on account of the limitation that may exist in the period over which the males are in possession of ripe sperm and are in a condition to copulate. Direct evidence on the point is slight, but so far as is known it would appear that the males in most species of Pinnipedia tend to come into breeding condition well in advance of the date of birth of the first pups. For example, fighting among the male Weddell seals occurs even before the birth of the pups, and Hamilton (1934) for the Southern Sea Lion, states that the bulls take an interest in the young cows as early as August, when the pupping time is not until near the new year (i.e. midsummer). Having come into condition well in advance of the time when the females require their services, there is some evidence, for example in the Weddell seal, that sperm production begins to diminish soon after the normal mating time. It may be argued that in a species where this gradual progression in the pupping time of the individual female occurs, the time of sperm production in the males would have become prolonged and this may well be so. But where the polygynous system is well-developed it can scarcely be assumed that the period during which the harem bulls can remain continuously active at their stations can be much further extended. The worn-out condition of the big bull Elephant and Fur seals after 6 or 7 weeks or even more of almost continuous fighting for possession of the cows, and frequent copulation, is well known. During the whole of this period the harem bull is without food and maintains his enormous bulk and intense activity at the expense of his blubber. That such exertion could be much further extended is highly improbable. The old cows that pup at the later dates are very possibly served by bulls that have been forced to be idle earlier in the season and only now, when the harem bulls have become exhausted, can they belatedly make use of their sexual powers.

Should the annual female retardation be still greater, or the males less capable

of sperm production late in the season, it is clear that after the first few years of her breeding life, the female will pup so late that she will fail to become pregnant again that season. When this happens probably she will be one of the first to be served in the following year when the cyclical process of gradual retardation can begin again.

It is apposite at this point to quote Hamilton's finding for the Southern Sea Lion (1939, p. 154). "It appears that in spite of the occurrence of a quite well-defined breeding season there is no division of the year into oestrous and anoestrous periods. On the contrary, *Otaria*, as a species, is sexually active all the year round. Since neither sex has periods of functional sterility the reason for the contraction of the breeding season into a comparatively short time in summer is obscure."

The Walrus is the only Pinniped in which so far as we know the females do not breed every year. The period of gestation is stated by Chapsky (1936) to be about a year, the mating season to be approximately coincident with the pupping season, and lactation to last some 18 months. The lactation period is thus enormously longer than in any other Pinniped. Only half the adult females are said to be pregnant at any one time, so presumably pupping takes place in alternate years, in which case, despite the delay of a year, the new pregnancy will still overlap a few months with the last lactation. The prolonged lactation may in itself be a cause of the breeding only in alternate years, since if pupping were annual and lactation 18 months, the females would become encumbered with two pups at the same time. On the other hand the prolonged lactation has perhaps only become possible because pregnancy is missed. The underlying cause may well be that gestation and the period before the female can ovulate again total so much over a year that no bulls are left capable of serving the post-parturient cows. In most species of Pinniped, however, gestation is sufficiently less than a year for the extreme regularity of pupping, so characteristic of the group, to be developed and maintained.

The argument now turns to the actual relationship between the sexes at the breeding places, and the presence or otherwise of a well-developed harem system. Necessarily the harem system can only flourish where the females are concentrated, and is impossible where the females are few in numbers or scattered over a large area.

When the females are concentrated it is clearly probable that a bull will attempt copulation with several cows. Should the cows refuse to take him at first it is to be expected that the bull would make some effort to keep close at hand, and would attempt to herd a group of cows together until they are ready for copulation. Such a herding together of females may be readily accomplished on land. Thus is initiated the harem system with all its corollaries; the strongest bulls obtaining the biggest harems and fathering the greatest number of pups; the idle bulls attempting to poach cows and so provoking constant fighting; and the evolution of disparity in size between the sexes.

Nutting (1891) has discussed 'Some of the Causes and Results of Polygamy among the Pinnipedia'. He starts by pointing out (p. 103) that true polygamy is rare among the Mammalia. "It must not be confused with mere promiscuous sexual intercourse, such as is often met with among the Herbivora. The term polygamy, in its strict sense, can properly only apply to those species in which a single male habitually copulates with several females, and jealously and persistently defends them from the approach of other males." The term 'polygyny' is preferable to

'polygamy'. Nutting then cites a number of species among the Pinnipeds which seem to illustrate the parallel growth of the harem habit and sexual disparity in size and temperament. He endeavours (p. 111) "to account for the following peculiarities met with among the Pinnipedia:

- 1st. The relation between great sexual disparity in size and polygamy.
- 2nd. The manner in which polygamy may have originated.
- 3rd. The origin and effect of excessive pugnacity.
- 4th. The origin and advantage of great sexual disparity.
- 5th. The origin and advantage of the ability to endure long-protracted fasts."

Nutting concludes by saying that "up to a certain point pugnacity and disparity seem to have acted as causes of polygamy. Beyond that point they seem to be effects of polygamy, or at least are accelerated or intensified by it."

The series of species cited by Nutting are the Walrus, where the sexes are approximately equal in size, peaceable and monogamous; the Hooded seal, where the male is considerably larger than the female, but is probably monogamous despite the fighting between the males; the Bearded seal, where the male weighs $2\frac{1}{2}$ times the female, and there are severe battles among the males, and the species by repute is polygynous. (Chapsky and Kovolev (1938) deny this.) From these Nutting proceeds to the Elephant seal, and Steller's Sea Lion, and thence to the Northern Fur seal, where the fully adult male may weigh even 6 times as much as the female, and which is the mammalian species in which polygyny reaches its highest perfection. "A consideration of the above series will disclose the fact that there is a close and constant relation between polygamy and disparity in size among the Pinnipedia . . . and that the combativeness of the males increases *pari passu* with the sexual disparity and polygamy" (p. 106).

The accumulation of information since Nutting's paper was written has not altered the truth of his conclusion. There is one point, however, which Nutting has not mentioned in his analysis of Pinniped polygyny. In the view of the present writer the most important single factor in the formation and maintenance of the harem system in a species of seal lies in whether or not copulation takes place in or out of the water. Among the Eared seals so far as is known copulation only normally occurs on land, though Allen (1880) and Elliott (1881) give instances of it occurring in the water in the Northern Fur seal. Among the more perfectly aquatically adapted Phocidae, with individual exceptions, copulation normally takes place in the water. Parallel with these facts are those already mentioned that the harem system tends to be present in all the Eared seals (where the species is present in sufficient numbers) while among the True seals it is only completely developed in the Elephant seal, which is the only Phocid known invariably to copulate on land. It is clear that the whole harem structure will tend to disintegrate if copulation can occur in the water. Possibly this has happened in the evolution of the Hooded seal, where there is a considerable size disparity and the males are fierce fighters. The females in this species tend to collect together on the ice to pup and the simultaneity of parturition is well marked. Copulation, however, always occurs in the water so far as is known, and though a male Hooded seal may be seen with a small group of cows and their

pups, there seems to be no day-to-day stability in the system warranting the term polygyny.

The Grey seal is a species in which it would seem that the harem system is at present in a process of disintegration, though the process probably has started at a comparatively late date. In this species copulating on land and in the water appear to occur about equally often. Fraser Darling (private communication) has made the first extended observations on the breeding behaviour of the animal, and these directly bear out the disintegration hypothesis. The sexual disparity in size is considerable (for example, the adult male skull weighs about twice as much as that of the adult female) though scarcely approaching the disparity found in the Fur and Elephant seals. In the season, which seems to be more extended than in any other species, the adult bulls haul out first and take up station on the breeding grounds. The cows later emerge, but the bulls have no control over them, allowing them to wander back to the sea or away to an adjacent bull. The harem system is 'vestigial', the bulls having well-marked territorial instincts but no real control over the cows. There is a certain amount of fighting between the males early in the season, but there is none of that jealous guarding of the harem so typical of the more truly polygynous species. In addition, the bulls frequently seem to lose interest in their station after some weeks' occupation and then move off, another bull occupying their former position and copulating with whatever cows present themselves. There can be little doubt that the truly polygynous habit, which in the past was the cause of the sexual disparity in size and behaviour in the species, is now in process of decay due to the growing incidence of aquatic copulation.

Similarly in the Bearded seal there is a sexual disparity in size, in favour of the male, of about the same magnitude as in the Grey seal. The Bearded seal has usually been stated to be somewhat polygynous, but Chapsky and Kovolev (1938) deny this, and state further, on the authority of hunters, that copulation can occur in the water *or* on the ice.

Amongst most other species of Phocids the disparity in size between the sexes is slight, though present knowledge is far from adequate. The antarctic Phocids are peculiar in that among all of them, the Leopard, the Weddell, the Crabeater, and the Ross, the female tends to grow to a somewhat larger size than the male. This disparity is rather more marked in the Leopard (Hamilton, 1939) than in the other three species, though knowledge of the Ross seal is based on quite inadequate figures. Whether or not these species of antarctic Phocid have passed through a strictly polygynous phase in their evolution can only be surmised, but it seems improbable. The relationships of the southern Phocids with those of the north are obscure, and there are no obvious inter-connections. The polygynous Elephant seal of the sub-antarctic zone has, however, a much closer connection with the northern seals, being clearly related to the Hooded and being classed with it in the sub-family *Cystophorinae*, the male in both being the larger.

The mating behaviour of these southern Phocids is almost unobservable, and certainly at present there is no further information than that the female tends to be the larger, and that copulation is almost certainly in the water. The Leopard seal is a solitary wanderer, the Crabeater tends always to be somewhat gregarious, the Weddell seems not to be truly gregarious except at the pupping time, while the Ross

seal appears (in our ignorance) to be solitary. It would seem most probable that in all four species copulation is promiscuous, the males and females being present in the same area at the same time, and so far as we know, in roughly equal numbers, and that what fighting does occur between the males has little important significance. The sexual capacity of the bulls in these species is quite unknown. The adult male of the Northern Fur seal can apparently maintain and cover a harem of as many as 70 cows, though the practice at the Pribilof Islands is to arrange for an average harem of more nearly 40 cows. The polygynous bull Elephant seal sometimes may have 30 cows. It is reasonable to suppose that in these promiscuous southern Phocids the bull can impregnate a considerable number of cows if opportunity offers. Whether the opportunity ever does offer in nature is unknown, but the bull's ability in this direction is clearly important in any consideration of possible controlled utilization of the stock of animals for skins or blubber.

SUMMARY

THE biology of the Weddell and Crabeater seals is described in detail. Both are circumpolar antarctic forms.

THE WEDDELL SEAL, *Leptonychotes weddelli* (Lesson) is non-migratory and coastal in its habit. The food of the adult is fish and Cephalopods, while crustaceans form the main diet for a short time after the end of lactation. The young animal enters the water for the first time at an age of about 3 weeks. During the first 2 years of life the Weddell seal rarely leaves the water and consequently is taken in very small numbers. The adult animals lie out on beaches or on fjord ice, but the great majority of the individual's life is spent constantly in the water. The animals winter beneath the unbroken ice of bays and fjords, keeping open breathing-holes by sawing with the teeth.

The pup is born in a woolly coat that begins to be moulted at the age of about 2 weeks. The older animals moult each year in the summer months. Feeding does not cease during the moult. The Weddell seal is normally silent but is able to emit a variety of sounds, especially in the breeding season.

The amount of fighting in the Weddell seal is not great, nor is it entirely confined to the males. The head, axilla, and genital orifice are the normal points of attack. Most of the fighting between the males occurs just before the pupping time.

The dentition of seals has many peculiar features. In both the Weddell and the Crabeater, X-ray examination has shown that the milk dentition reaches its maximum size in the fourth month of pregnancy when the foetus is rather over 30 cm. long. The milk dentition is then reabsorbed and the permanent dentition, which is already just appearing in the fourth month, is beginning to erupt at the time of birth. The average age at which the pup attains its full dentition is 34 days from birth, this being before the end of lactation. X-ray examination shows that of the 5 permanent post-canines 3 only are preceded by milk-teeth, so that the last 2 post-canines should be considered as true molars. The presence of a sixth post-canine in the upper jaw is by no means rare in the species. The post-canine teeth

function simply as grasping pegs, and normally persist throughout the life of the individual in almost perfect condition. The anterior teeth, particularly the canines and the caniniform second pair of upper incisors, are used for ice-sawing, and suffer considerable damage as a result through wear and fracture. Once the pulp cavity of one of these teeth becomes exposed, rapid necrosis sets in with widespread damage to the bone. This damage, and loss of teeth due to necrosis, is considered probably to be the most potent single cause of death in the species, the individual failing to keep open adequate breathing-holes in winter beneath the fast-ice.

The Killer whale is not an important factor in the life of the species.

Copulation has never been seen in the Weddell seal and almost certainly always takes place in the water. In Graham Land copulation probably takes place from about the middle of November to the middle of December. By January the males are going out of condition and their testes cease to contain ripe sperm. Gestation is probably a few days less than 10 months, this being deduced from examination of the ovaries, by the shape of the growth curve of foetal sizes, and the observed time of pupping. The whole reproductive cycle is about 1 month later in the Ross Sea than on the west coast of Graham Land.

The pregnant seals collect into groups on the fast-ice to pup. In any one area all the pups are born within a period of 4 to 5 weeks with a well-marked peak within that period. Parturition is rapid, and the umbilical cord is severed by the young seal breaking it at birth. A single pup is the rule, but rare cases of twinning have been observed.

Owing to differences in lying out habits, the only times at which the animals can be sexed, a sure determination of the adult sex ratio is not possible. It is probably not far from unity, but there is some evidence to show that male pups are produced in rather greater numbers than female.

Lactation lasts about 7 weeks, and permanent separation of the young from their mothers occurs at about the same time. The average weight of the Weddell pup at birth is 64 lb., and its length 45 in. to 50 in. Growth is extremely rapid, often being as much as 7 lb. per day, and the weight at birth is doubled by the end of the second week. After the end of lactation there is some decrease in the body weight of the pups.

The blubber thickness of the adults is from $1\frac{1}{2}$ in. to 3 in., being thickest in the females at the end of the winter, before pupping. The weight of a full-grown female in good condition may be over 900 lb.

All Weddell seals killed in the same month in any year must be either of the same age, or be separated by an exact number of years. On this basis attempts are made to define the age classes in order to determine the composition of the population. Separation of the year classes by observation of the living animals is not possible except in so far as the individuals less than a year old can be distinguished from all those of greater age. Three main methods of possible definition of year classes are considered. These are body lengths, skull dimensions and appearance, and ovarian examination.

There is a well-marked tendency for the largest female seals to surpass the largest male seals in body length. Very few males are more than 100 in. long, while females of greater length are by no means rare. A female at 115 in. was the longest

seal measured. Owing to variations in the growth of the individuals it is not possible certainly to separate the age groups by this criterion beyond the middle of the second year.

The skulls of male and female Weddell seals can be distinguished in less than 50 per cent of cases on their own characters alone.

As with the body length, skull dimensions are not sufficient alone to separate the year classes beyond the middle of the second year. The closure of the basioccipital-basisphenoid suture usually marks the distinction between the skulls of the second- and third-year groups. The extent of the closure of the palate sutures is probably an indication of relative ages in the older skulls.

The female seals are pregnant for the first time in their third year, being impregnated at about the age of 26 months.

The corpus luteum in the Weddell seal remains of large size until the end of pregnancy. After parturition it diminishes greatly in size but long remains as a visible entity in the ovary. The great majority of female Weddells ovulate only once, and that successfully, in each year. There is a well-marked correlation between the lengths of the individual female seals and the number of corpora in their ovaries. The frequency distribution of the different numbers of old corpora recorded in a series of ovaries is used as evidence to prove that each corpus forms a permanent record of each pregnancy. It follows that the approximate age in years of the normal female is obtained by adding the 2 years of her pre-adult life to the number of corpora in her ovaries. It is concluded tentatively that not more than 16 per cent of the sexually mature females fail to become pregnant in any one year.

A broad correlation is found between body lengths, skull dimensions and characters, and the number of old corpora in the ovaries. A series of female skulls, all taken in January, is used as a basis for the determination of age classes by means of a combined use of these three criteria. It becomes clear that the 4-month and the 16-month skulls are separable from each other and from all older by dimensions and appearance. The 28-month skulls are also separable from those both younger and older by appearance and state of the sutures, but not by size alone from those older. The '40-plus'-month skulls are likewise separable from all those younger by appearance and sutural condition; but the division of these older skulls into groups by any means other than ovarian evidence is doubtful. Working from this series of female skulls taken from seals killed in the same month of the year, other skulls, it is believed, can be assigned fairly accurately to their correct age groups. From this point of view there is no evidence that the male and female skulls differ in any important respect.

The apparent age composition of the Weddell seal population is then considered. It is evident that true sampling of the population requires the lying out habits of the two sexes and of the different age groups to be exactly similar, since the animals can only be taken when they are out of the water. It is known, however, that the lying out habits are not always the same, and therefore analysis of the apparent age composition of the population must proceed with extreme caution.

There is no evidence to suggest that the age distribution of the male seals differs greatly from that of the females. It seems probable, from a tentative analysis of the population, that about 50 per cent of the female pups born must attain sexual

maturity to keep the population constant, and that the apparent size of the older age groups is consistent with the view, based on ovarian evidence, that few females survive to pup more than six times.

THE CRABEATER SEAL, *Lobodon carcinophagus* (Jacquinot & Pucheran), is treated along the same lines as the Weddell, frequent comparisons being made with that species. The Crabeater is an animal of the offshore pack-ice and is at least semi-migratory. There is a great influx of the animals into the coastal waters west of Graham Land at midsummer. There is a similar influx of Crabeaters in the summer months into the southern part of the Ross Sea, this influx consisting for the most part of young individuals.

The normal diet of the species at all stages of its life history consists of Euphausiids which are filtered from the water with the aid of highly-specialized, many cusped, cheek-teeth.

The Crabeater pups offshore in the pack-ice. As a result, the members of the *Belgica* and *Endurance* Expeditions are the only people to have seen the pups in the first 3 months of life. It is probable, but not certain, that the pup moults its natal woolly coat within a fortnight of birth and enters the water within the same short period.

Though normally Crabeaters winter offshore in the pack-ice, it is shown that a very small number may remain beneath the fast-ice inshore. No Crabeater was found, however, whose caniniform teeth showed obvious wear by ice-sawing.

The adult seals moult in the summer months, the old coat previously having weathered to a silvery whiteness. The animals continue to feed during the moult.

The male Crabeaters evidently fight among themselves rather more than the females, but the amount of fighting in the species appears to be small. Nearly every Crabeater bears upon its body at least one set of long scars resulting from attacks by Killer whales, and it is highly probable that these animals are the main cause of mortality in the species.

The milk dentition of the Crabeater seals appears and disappears in the same way as it does in the Weddell. The vestigial milk dentition shows only a trace of the complex adult cusping of the post-canine teeth. In the Crabeater seal supernumerary teeth are extremely rare, as are other dental abnormalities, compared with the Weddell. There is some tendency to produce a still greater number of cusps in the post-canine teeth. It is evident that injury of any of the teeth in the Crabeater seal is extremely uncommon, and that when it does occur the results are far less serious than in the Weddell, tooth breakage rarely leading to extensive necrosis.

Knowledge of the various phases in the reproductive cycle of the Crabeater is scanty. A good deal may be deduced by analogy with the Weddell. Copulation in the Crabeater almost certainly takes place in the water. A growth curve for the Crabeater foetus is presented which shows that copulation in this species is probably about a month later than among the Weddells in the same area, and that there is a little more variation in the size of the foetus at any one date than in that species. The period of gestation in the Crabeater is shown to be probably 9 months, conception taking place in December and pupping in September.

There is insufficient data to draw conclusions as to the sex ratio in the species,

but there is no evidence to suggest that it is far from unity. Lactation is probably short, perhaps only a few days, but the evidence is slight.

The size of the Crabeater pup at birth is probably about the same as that of the Weddell. Growth in the first 3 months is extremely rapid, the animal even being capable of reaching a length of 6 ft. in this period.

The blubber thickness of the Crabeater seal as seen in the summer months is from 2 in. to $2\frac{1}{2}$ in. The weight of the adult animal is probably about 500 lb. The Crabeater is a more lithe and active animal than the Weddell, and probably weighs in most instances about two-thirds as much as the latter animal at the same body length and in the same relative condition of fatness.

As for the Weddell seal, similar attempts by similar methods have been made with the Crabeater to determine the age groups. In the Crabeater the sexual disparity in size in favour of the females is of about the same order as in the Weddell. The largest Crabeater taken was a female of 103 in. No certain sexual distinction can be made from general observation of the living animals, though the males tend to have a larger head and a greater abundance of small scars on the head and shoulders.

A study of the figures for body length show that the young animals grow extremely rapidly, and that even the distinction between $\frac{1}{2}$ -year-old animals and those of greater age may not always be completely clear on this criterion. The body length figures, in combination with those of percentage pregnancies by length groups, strongly suggest that some, but probably not all, of the young female Crab eaters may become pregnant for the first time in their second year, having conceived when 15 months of age. Thus, some at least of the female Crab eaters become sexually mature a full year earlier than the virgin Weddells.

It is possible to distinguish the skulls of the two sexes with a fair degree of certainty from their general appearance. The male Crabeater tends to have a longer skull than the female at the same body length. From the study of skulls and body lengths it is possible to distinguish $\frac{1}{2}$ -year-old seals from $1\frac{1}{2}$ -year-old animals fairly accurately on a dimensional basis, while the further distinction between $1\frac{1}{2}$ -year-old seals and ' $2\frac{1}{2}$ -plus'-year animals can be made from the skull sutures and appearance with sureness for the males, with less certainty for the females.

The ovarian evidence for the Crabeater is much less complete than for the Weddell. It seems most probable however, that the Crabeater resembles the Weddell in producing a single ripe ovum annually, at least 80 per cent of the sexually mature females becoming pregnant every year. The corpora seem to persist throughout the life of the individual. The ovarian evidence, so far as it goes, bears out the conclusions reached above as to the separation of the early age groups of the two sexes. It then becomes clear that the proportion of ' $2\frac{1}{2}$ -plus'-year-old seals among those Crab eaters that were killed in Graham Land, is unduly small, and can by no means represent their true strength in the population as a whole. It is concluded that the coastal influx of Crabeater seals in the summer months on the west coast of Graham Land includes a disproportionately large number of the younger animals. This is similar to what has been observed in the southern part of the Ross Sea, but there the first-year animals make up so much as two-thirds of the total seals that move into the inshore waters.

THE COMPARATIVE BEHAVIOUR OF THE PINNIPEDIA

This is considered as a whole, including a comprehensive discussion of a variety of phenomena, in particular precocity, polygyny and the fixity of the breeding cycle. Copulation normally taking place on land is stressed as being the keystone of the polygynous system among Pinnipedia. Once the animals become so aquatically adapted that copulation can easily occur in the water, the harem system must disintegrate. The Elephant seal is the only truly polygynous Phocid, and it is the only Phocid that always copulates on land rather than in the water. The nicety of adjustment in the different species, whereby gestation plus the period between parturition and the next impregnation just equals a year, is brought out by a consideration of a variety of species.

In an addendum is set out in tabular form a summary of the bionomics, so far as they are known, of all the species of Pinnipedia in the world.

In a second addendum there is some consideration of the possible commercial exploitation of the Weddell and Crabeater seals, together with certain preliminary recommendations for its control.

A bibliography is provided.

ADDENDUM I

A COMPARISON OF THE BIONOMICS OF THE PINNIPEDIA OF THE WORLD

Allen (1880) provided what was almost a monograph of the known facts about the various species of seals, and his account is still by far the most complete. In the course of the present work on the Weddell and Crabeater seals, it is believed that practically all the relevant, modern literature has been noticed. It therefore seems worth while to provide in a condensed form the present knowledge of the main biological features of all the species of seals. The detailed synonymy of the various species has not been studied, and the Latin names given are those which seem to be in most general use. There are still very considerable gaps in the information: for example, the precise number and distribution of the various southern Otariids is still by no means certain. The gaps in present knowledge are the more surprising when considered in relation to the commercial importance, large size, and great numbers of many of the species concerned. (*See Table attached.*)

ADDENDUM II

A NOTE ON THE POSSIBLE COMMERCIAL EXPLOITATION OF THE WEDDELL AND CRABEATER SEALS, WITH A SUGGESTION FOR ITS CONTROL

Knowledge of the Weddell and Crabeater seals, though still by no means complete, is now far in advance of that of any other species of Phocid, not excluding the Harp

[illegible]

seal of which a total of about 500,000 are killed annually for skins and blubber. The extension of commercial sealing to Antarctic waters in the future, though not certain, is by no means improbable. It is therefore worth giving some consideration at the present time to those factors whose interplay may determine the ultimate fate of the Weddell and Crabeater populations.

The basis of commercial exploitation of this stock of southern seals is likely to be three-fold, the object being to obtain:

- (a) Blubber for the extraction of oil.
- (b) Adult skins for the making of fine grained leather.
- (c) Pup skins (before the juvenile moult) for clothing.

One of these may or may not take precedence over the others, but it is improbable that blubber alone would ever be the chief aim of the fishery, the supplies being moderately small, at a great distance from centres of population, and the hydro-genation of vegetable oil being increasingly easy of application.

The success of any southern fishery would depend upon the expectation of high prices for the adult and juvenile skins, the latter probably being individually the more valuable. In the case of the less valuable adult skins for transformation into high-grade leather, the price per skin would, within wide limits, probably be relatively independent of the number of skins placed on the market. On the other hand, the high prices realized for the pup skins, whose use is in women's clothing, might decrease very rapidly with an increase in the number of skins available. Thus an enlargement of the fishery for pup skins might perhaps not be so advantageous to its promoters as would an enlargement of a fishery for adult skins.

That adult skins and blubber of the Crabeater can be obtained in large numbers with comparative ease was made abundantly clear by the exploits of the Dundee whalers and Larsen in the *Jason* in the 1892-93 season in the north-west corner of the Weddell Sea. The Crabeater skins, however, are almost always greatly reduced in value by the presence of the parallel scars inflicted by the teeth of the Killer whales.

Crabeater pups are still virtually unknown: the period before the juvenile moult is probably extremely short and pupping takes place in inaccessible regions in the pack-ice in a stormy season of the year. Therefore a southern Phocid fishery would probably have its main return from adult and juvenile Weddell skins and the blubber of the adults of both species. The extraction of lower grade oils and the production of guano from the carcasses might also be practicable. It is evident that the Weddell seal, which is always a far less abundant animal than the Crabeater, would probably be the main object of any antarctic fishery.

In considerations such as these the size of the total populations of the two species of seals in the different areas is of great importance. But in the present state of knowledge it is quite impossible to produce even an approximate estimate upon which the most scanty reliance can be placed. It is apparent, however, that the potential rate of increase of the stocks is probably small. On the other hand, both species of seals are circumpolar, much of the stock is always likely to be inaccessible to commercial exploitation, and in the case of the Weddell, there is probably little individual wandering from one area to another.

For this reason no serious permanent effects on the stock as a whole are probable, if through ignorance or lack of proper control, exploitation of the stock in the more accessible areas is too vigorous. Thus it might be possible by trial-and-error in particular areas to obtain some information as to the amount of utilization that the stock could stand, and when this is found, to act accordingly in regulating any extension of the fishery.

The sex ratio in the Weddell and Crabeater seals apparently is not far from unity (with a possible bias in favour of greater numbers of males).

It seems certain that the Weddell seal, at least, is promiscuous, and probably some reduction in the number of the males would not seriously reduce the chances of each female becoming pregnant each year. Efforts might therefore be made with advantage either to restrict the commercial killing of seals to the males, or at least to attempt to make them bear the main burden of the fishery. It may be thought to enforce this regulation would be quite impossible from the practical point of view, since the skins and blubber of males and females are as indistinguishable from one another as are the seals when alive, until the underside of the body has been examined.

It is suggested however that adequate supervision might quite simply be obtained by inspecting all skins and confiscating those unaccompanied by an *os penis*. Likewise, regulations could be enforced requiring the production of one penis bone with a statutory weight of blubber. The penis bones would of course be destroyed in every case by the supervising official.

It is normally quite easy to make the individual Weddell or Crabeater seal roll over on its back so that it may be accurately sexed before being killed. The pups may be handled with fair ease, so that even among them, where the genital orifice is less obvious, sexing of the individual can soon be learnt by an untrained man. These facts, together with the above suggestions regarding the *os penis*, it is believed would allow of a rational control of the use of the stock of the Weddell and Crabeater seals.

ADDENDUM III

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A × 4.



× 3.9. B



A × 4.



× 3.7 B

THE MILK DENTITION OF THE WEDDELL AND CRABEATER SEALS

The two species of seal seem closely to resemble one another in the development of their teeth at the same foetal body length. The present series of photographs are from foetuses varying in body length from 230 to 500 mm. and approximately cover the passage through the two middle months of pregnancy.

(A) Weddell. 230 mm. First appearance of the milk dentition. The complete set (I 2/2, C 1/1, PM 3/3) is visible in the lower jaw, but the greater thickness of tissues to be penetrated makes the premolars almost invisible in the upper. In both jaws the first pair of incisors, as in the adult set, are extremely small.

(B)—Crabeater. 310 mm. The complete milk dentition is visible in both jaws. At this stage the second pair of upper incisors is bigger than the canines.



A × 3.



× 3. B



A × 3.



× 3. B

(A)—Weddell. 330 mm. The permanent canines are now becoming visible in both jaws, and the permanent incisors in the upper.

(B)—Crabeater. 335 mm. The permanent canines are visible in both jaws, and the permanent incisors in the upper. In the upper jaw particularly, the space later to be filled by the 4th post-canine tooth is now plain.



× 1.



× 3.



× 3.

Crabeater. 360 mm. The inner pair, above and below, of milk incisors is now being reabsorbed and is extremely small. The milk post-canines have reached their maximum size, and it is clear that they are only three in number. In side-view the slight cusping of the third milk post-canine is obvious.



$\times 1.$



$\times 1\frac{1}{2}.$

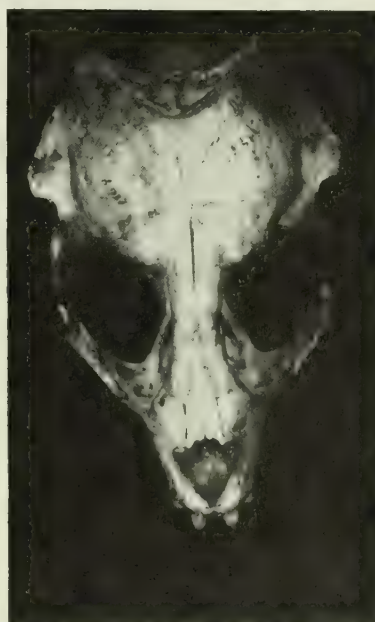


$\times 2\frac{1}{2}.$

Weddell. 500 mm. The full milk dentition is still visible, though reabsorption is proceeding rapidly. None of the milk post-canines is cusped in this species. The permanent post-canines are now becoming visible in the lower jaw.



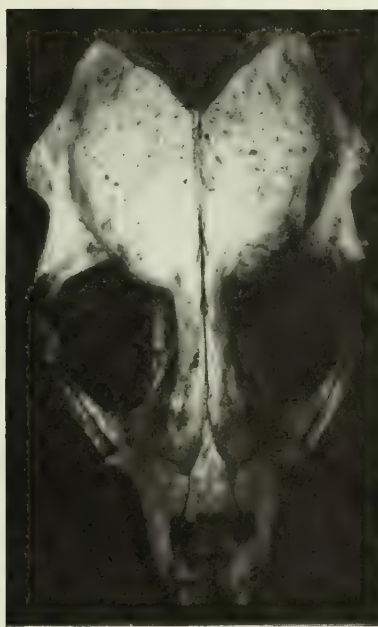
A



B



C



D

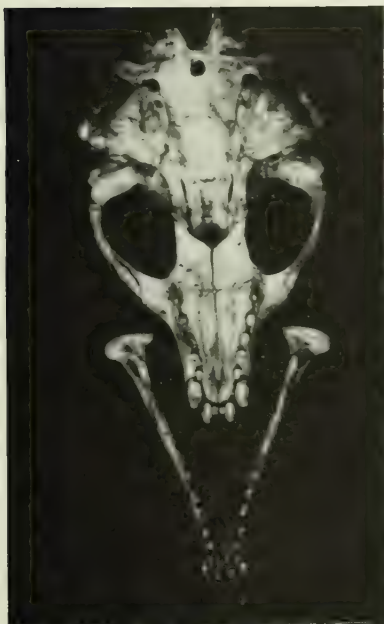
Skulls of female Weddell seals. Dorsal aspect. (A)—No. 137, age 4 months. (B)—No. 113, age 16 months. (C)—No. 138, age 28 months. (D)—No. 100, age 40 months.



A



B



C

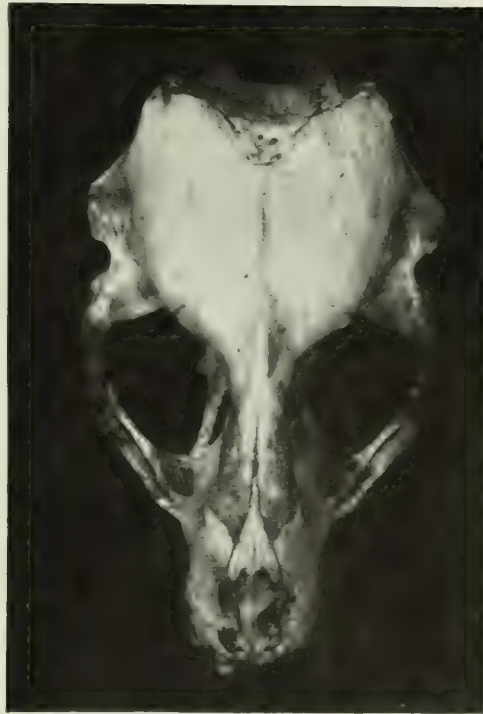


D

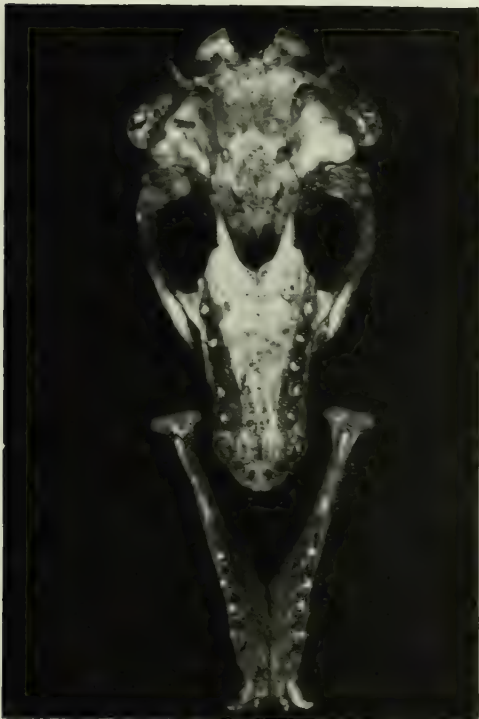
Skulls of female Weddell seals. Ventral aspect. (A)—No. 137, age 4 months. (B)—No. 113, age 16 months. (C)—No. 138, age 28 months. (D)—No. 100, age 40 months.



A



B



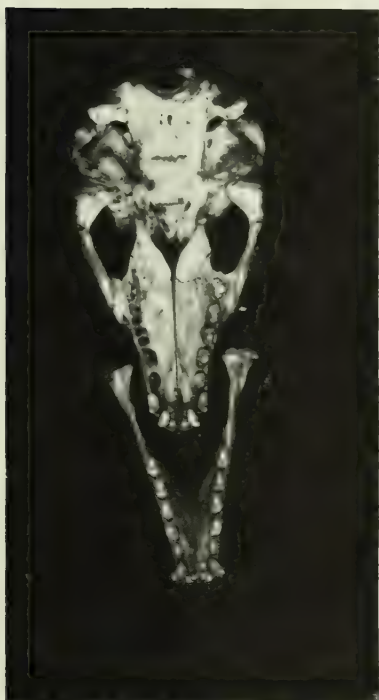
The skulls of (A) an old male Crabeater, and (B) an old male Weddell (Nos. 93 and 56 in the Graham Land series). (A) is the single case of considerable tooth fracture found among the Crabeater seals and it is also the skull in which fusion of the palatal sutures has proceeded farthest. There has been no serious necrosis consequent upon the tooth fracture. In (B), on the other hand, the tooth-wear and fracture has been followed by serious necrosis and drainage channels can be seen above and below.



A



B



Male Crabeater skulls. Dorsal and ventral aspects. (A)—No. 1, age 7 months. (B)—No. 10, age 17 months.



(Above)—Adult female Weddell with week-old pup. (Below)—Year-old female Weddell seal.



Photograph by Brian Roberts



Photograph by A. Stephenson

(Above)—Young male Crabeater with deep suppurating wound on neck. (Below)—Crabeaters on a floe in late summer. The light-coloured seals have not yet moulted. Several animals exhibit the scars from the attacks of Killer whales.

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THE
LIFE CYCLE OF WILSON'S PETREL
OCEANITES OCEANICUS (KUHL)

By

BRIAN ROBERTS, M.A., Ph.D.
Scott Polar Research Institute, Cambridge

WITH SEVEN PLATES AND TWENTY TEXT FIGURES

LONDON

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Scott Polar Research Institute, Cambridge

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HISTORICAL NOTES AND INTRODUCTION

WILSON'S PETREL (*Oceanites oceanicus*) was first described in 1813 by Alexander Wilson. He supposed it to be identical with the British Storm Petrel (*Hydrobates pelagicus*), and thought it bred in the West Indies and on the coast of Florida. In 1820 Heinrich Kuhl named it *Procellaria oceanica* from a specimen in Temminck's collection, and to his description he referred an unpublished drawing of the species by Sidney Parkinson, artist of Captain Cook's First Voyage. This drawing was made as long ago as December 1768 from a bird taken in the South Atlantic, off the

Rio de la Plata, and is preserved in the British Museum (Nat. Hist.). Wilson's Petrel has, in fact, been known for more than a hundred years as a common bird of the North Atlantic Ocean, but its true distribution and breeding places have only recently been discovered.

In 1824, Bonaparte named the form occurring in the North Atlantic *Procellaria wilsoni*, and this was for long thought to be distinct from Kuhl's *P. oceanica* of the South Atlantic. Audubon (1840), and others, must have confused it with Leach's Petrel (*Oceanodroma leucorhoa*), for they believed that it nested in Nova Scotia. Brewster (1883) shot a number of Wilson's Petrels in the Gulf of St. Lawrence between the dates 17 June and 25 July. After examining their undeveloped gonads, he concluded that "they breed in winter or early Spring in tropical or sub-tropical regions and visit the north-eastern coast of the United States *only in the interim between one breeding season and the next.*" He was thus the first to come near to the truth, but did not put the breeding place far enough to the south.

It was the Rev. A. E. Eaton, a member of the British Transit of Venus Expedition of 1874, who obtained the first definite knowledge of the true breeding of Wilson's Petrel in the Antarctic. He found on Kerguelen Island 9 nests with eggs which were described with his other collections by Sharpe (1879). The second edition of the A.O.U. Check List, published in 1895, gave Kerguelen Island as the only known breeding place of this bird, but when other Antarctic breeding localities were discovered at the beginning of this century, *wilsoni* came to be accepted as a synonym of *oceanicus*, and it was suspected that the birds breeding in the far south ranged northwards during the Antarctic winter and northern summer. As late as 1912, however, Mathews stated his opinion that this was an unsatisfactory explanation, and he "confidently anticipated the discovery of breeding colonies of a subspecies of *O. oceanicus* in some of the West Indian or North African islands." It remained for Murphy (1918) to prove conclusively that the birds of the North and South Atlantic are all of the same species, and that there is an annual migration to the northern ocean from breeding grounds in the far south.

Thus in 1934, although the eggs of Wilson's Petrel had been known for 60 years, and many other Antarctic nesting localities had been found since Eaton's time, practically nothing of their breeding habits had been discovered owing to the impossibility of making anything more than casual observations during brief visits to the nesting areas.

During the British Graham Land Expedition of 1934-37 we were most fortunate in having a small, accessible colony of Wilson's Petrels close to our northern base-hut in the Argentine Islands. Moreover, the birds in this colony were nesting in shallow burrows in a patch of moss instead of in the more usual situation in a crevice or among shattered rocks, and this made it possible to excavate the nests without disturbing the birds. My observations at this colony, extending over three seasons, and at other localities in West Antarctica and the Atlantic Ocean, now enable me to give a fairly comprehensive survey of their habits and breeding biology. The object of this paper is to describe these observations, and to bring together a summary of other records in order to provide an account of the whole life cycle of the species.

My indebtedness to other workers during the preparation of parts of this paper will be apparent from the lists of references on p. 177 and pp. 193-4. At the same time

I take this opportunity to acknowledge much help from my companions of the Graham Land Expedition, and especially from Dr. Colin Bertram, who was always ready to assist me both in the Antarctic and at home. I am greatly indebted to Dr. R. C. Murphy, who generously sent me a copy of the notes on *Oceanites* which he had prepared for his forthcoming book on Petrels. These notes contained the essential details of specimens in the American Museum of Natural History, and have enabled me to extend the discussions on taxonomy and migration. I also wish to thank Mr. N. B. Kinnear and the staff of the 'Bird Room' at the British Museum for help in elucidating various points; Dr. F. H. A. Marshall and Mr. H. F. Witherby for their advice while preparing the manuscript; and Mr. John Wright for assistance in the statistical treatment of measurements in the section on taxonomy. The preparation of this paper has been made possible by grants from the Department of Scientific and Industrial Research and from Emmanuel College, Cambridge.

The original field notes upon which this study is based have been deposited at the Scott Polar Research Institute, Cambridge.

BREEDING LOCALITIES

The following is a list of the localities in which Wilson's Petrel has been found breeding:

SOUTH VICTORIA LAND	Crescent Bay (Priestley, 1911). Cape Adare (Hanson, 1902; Wilson, 1907).
ADÉLIE LAND	Cape Denison, Mackellar Islets, Cape Hunter, Penguin Point (Falla, 1937).
QUEEN MARY LAND	Haswell Island (Falla, 1937).
MacROBERTSON LAND, ETC.	Murray Monolith, Scullin Monolith, Cape Bruce (Falla, 1937).
KAISER WILHELM II LAND	Gaussberg (Vanhöffen, 1905; Falla, 1937).
ENDERBY LAND	Proclamation Island (Falla, 1937).
GRAHAM LAND	Hope Bay (Lönnerberg, 1905; Andersson, 1908). Wandel Island (Ménégaux, 1907). Petermann Island (Gain, 1914; Roberts), Port Lockroy, Argentine Islands, Berthelot Islands (Roberts).
SOUTH SHETLAND ISLANDS	Gibbs Island (Strong, 1936-37), Harmony Cove, Admiralty Bay, Desolation Island (Hart, 1934-35). Deception Island (Gain, 1914; Roberts).
SOUTH ORKNEY ISLANDS	(Clarke, 1906; Ardley, 1936).
SOUTH GEORGIA	(Matthews, 1929).
FALKLAND ISLANDS	Jason Islands (Hamilton, 1939).

TIERRA DEL FUEGO

Deceit Island, Herschel Island (Reynolds, 1935; Murphy, 1936).

KERGUELEN ISLAND

(Eaton, 1875; Coues, 1875; Sharpe and Saunders, 1879; Hall, 1900; Vanhöffen, 1905; Falla, 1937.)



FIG. 1.

These are the localities in which breeding has been proved up to the present time (see Fig. 1). In addition, there are very many others at which breeding has been suspected, but not proved. It is probably true to say that almost every suitable exposed rock area of the coast of the Antarctic Continent is a breeding place of the species, and we may expect the same of the majority of off-lying islands.

Eggs have not yet been taken at Heard Island, but there is substantial evidence that Wilson's Petrels breed there (Moseley, 1879; and Falla, 1937). Macquarie Island has been well searched and appears to lie outside the breeding range. Satisfactory evidence is still lacking from Crozet, Marion, Prince Edward, Bouvet, and the South Sandwich Islands. Published records of breeding on Mauritius (Bent, 1922, and *A.O.U. Check List*, 4th Edition, 1931) appear to be without foundation.

TAXONOMY

In previous discussions of the taxonomy of *Oceanites* many of the specimens used have been taken during migration, and consequently their place of origin is unknown. The tips of the flight feathers become very much worn during migration and this gradual diminution of the tips invalidates the accurate comparison of

measurements from birds taken at widely differing dates and localities. Further difficulties have been introduced by the inclusion of moulting and immature birds. It has therefore seemed essential that any taxonomic discussion should be based solely on adults taken from their breeding localities, and that the identity of migrating specimens from northern latitudes should only be considered afterwards in the light of the conclusions reached.

In the following lists the wing measurements are from the carpal joint to the tip of the longest primary, the manus having been straightened out as much as possible. Tail measurements are taken to the end of the outer retrices; 'toe' refers to the length of the middle toe and claw.

Table I includes every bird *from the breeding localities* which I have been able to trace. The origin of the specimens is indicated so that, if necessary, they can be traced again.

A	Australian Museum, Sydney.
AM	Auckland Museum, New Zealand.
AMNH	American Museum of Natural History.
B	Brooklyn Museum.
BANZARE	British Australian and New Zealand Antarctic Research Expedition, 1929-31. (Specimens now in Auckland Museum.)
BM	British Museum (Natural History).
BGLE	British Graham Land Expedition, 1934-37. (Specimens in B.M.)
MM	National Museum, Melbourne.

TABLE I

(Measurements of *Oceanites oceanicus* in mm.)

SOUTH GEORGIA

Number.	Collector.	Locality.	Date	Sex.	Wing.	Tarsus	Tail.	Toe.	Culmen
AMNH.132479	R. C. Murphy	—	1.12.12	♂	147	34.5	66	28	13
B.10714	"	—	"	♀	150	36	60	26.5	12
AMNH.132480	"	—	30. 1.13	♂	146	34	61	28.5	12.5
AMNH.132482	"	—	6. 2.13	♂	154	36	60	28.5	13
AMNH.132481	"	—	"	♂	150	34	62	26.5	12
B.10718	"	—	"	♀	151	34.5	63	28	12
B.10717	"	—	"	♀	151	35	63	27.5	13
AMNH.132483	"	—	1.12.12	♂	148	35	64	28	12
B.10715	"	—	"	♀	149	36	60	26.5	13
B.10716	"	—	6. 2.13	♀	144	33.5	62	26	12
AMNH.132484	"	—	"	♀	148	34	61	28	12.5
B.11179	J. G. Correia	—	10. 2.14	♀	151	33	68	26.5	13
BM.1914.3.8.40	P. Stammwitz	—	2.12.13	♂	146	32	65	27.5	13
BM.1914.3.8.41	"	—	"	—	145	33	65	27	12.5

FALKLAND ISLANDS

BM.1932.7.2.27	Mrs. Jason Hansen	Grand Jason	8. 1.24	♂	138	34.5	65	28	12
BM.1932.7.2.26	"	" "	"	♀	134	33	62	26.5	11.5
BM.1932.7.2.25	"	" "	"	♀	136	34.5	64.5	29	12.5
BM.1932.7.2.24	J. E. Hamilton	Fox Bay	? 3.32	♂	139	34	64.5	27	11
BM.	"	Grand Jason	1. 3.35	♂	132	33.5	56	27	11.5
BM.	"	" "	"	—	142	33	63.5	28	12

BRITISH GRAHAM LAND EXPEDITION

SOUTH VICTORIA LAND

Number.	Collector.	Locality.	Date.	Sex	Wing.	Tarsus	Tail.	Toe.	Culmen
AMNH	N. Hanson	63° 41' S., 160° 16' E.	2. 1.99	+	159	34	72	28.9	12
BM.1901.1.7.33	"	66° 4' S., 166° 51' E.	19. 1.99	+	151	34	71	28	12
BM.1901.1.7.32	"	63° 43' S., 161° 6' E.	8. 1.99	+	159	34	72	28.5	12
BM1905.12.30.269	E. A. Wilson	Cape Adare	9. 1.02	+	155	33	74	28	12
BM1905.12.30.267	"	" "	"	+	157	34	75	31	12.5
BM1905.12.30.268	"	" "	"	+	151	33	69	27	12
BM1905.12.30.366	G. A. Davidson	67° S., 179° E.	25.11.02	+	149	33.5	66	31	12.5
BM1905.12.30.269	E. A. Wilson	Cape Aadare	9. 1.02	+	155	33	73	29	12
BM1905.12.30.268	"	" "	"	+	158	31.5	69	28	12.5
BM1905.12.30.267	"	" "	"	+	158	35	75	31.5	12

QUEEN MARY LAND AND MacROBERTSON LAND

A.22080	A.A.E.1911-14	Queen Mary Land	15. 1.13	+	157	35	71	27	12
A.22078	"	" "	"	+	153	33	66	28	12.5
MM.R5995	"	" "	"	+	152	32	69	27.5	13
MM.R5996	"	" "	"	+	159	33	71	28	12
BM.90.5.5.8	" Challenger "	65° 42' S., 79° 49' E.	14. 2.74	+	154	34	68.5	28	12
BM.80.11.18.681	"	" "	"	+	156	34	70.5	28.5	12
BM.80.11.18.679	"	" "	"	+	154	32.5	72	27	12
BM.80.11.18.67	"	" "	"	+	142	31.5	63	26.5	12
BANZARE.586	R. A. Falla	66° 11' S., 65° 10' E.	31.12.29	+	155	34	70	28	12.5
BANZARE.587	"	" "	"	+	151	34	66	27	12
BANZARE.588	"	" "	"	+	153	33	70	28	12.5
BANZARE.589	"	" "	"	+	153	33	65	29	12.5
BANZARE.1267	"	67° 10' S., 74° 28' E.	10. 2.31	+	162	35.5	72	29	13.5
BANZARE.1271	"	" "	"	+	164	35	75	30	13
AM.1202.1	"	" "	"	—	157	33	68	26	11.5

KERGUELEN ISLANDS

AMNH	R. Hall	—	14. 1.98	+	145	38	59	27	12
"	"	—	8. 2.98	+	150	35	58.5	27	12
BANZARE.1073	R. A. Falla	—	10. 2.30	+	149	33	58	26	12
BANZARE.818	"	—	"	+	141	35	57	27	11
BANZARE.1074	"	—	22. 2.30	+	145	34	60	27	12
BANZARE.1075	"	—	"	+	144	35	60	28.5	12
BANZARE.1025a	"	—	23. 2.30	+	139	32	60	28	12.5
BANZARE.1025b	"	—	"	+	147	34	58	27	11
BANZARE.1025c	"	—	"	+	144	34	61	26	12
BM.76.4.26.17	A. E. Eaton	—	—	+	141	34.5	62	28	12

SOUTH AMERICA

BM.1933.5.21.4	P. W. Reynolds	Deceit Is., Cape Horn	14.12.32	♂	139	35	60	28	12
AMNH	R. H. Beck	Wollaston I.	1. 1.15	♂	136	35.3	58.5	28	10.6
"	"	Morton I.	17.12.14	♂	139	34.4	58.5	26.5	10.8
"	"	"	"	+	138	—	56.3	26.4	10.9
"	"	"	"	+	142	35.5	61.6	27.7	10.3
"	"	"	"	+	143	35.1	60.4	26.8	11.1
"	"	Nassau Bay	4. 1.15	+	141	35	58.1	26.1	11.5
"	"	" "	"	+	137	34.7	54.5	27.2	10.8
"	"	" "	"	+	142	35.1	63.4	27	11.1
"	"	Punta Arenas	6. 3.15	+	143	35.3	59.8	28.4	10.8
"	"	" "	"	+	136	34	58.1	26.9	11.5

ADÉLIE LAND

Number.	Collector.	Locality.	Date.	Sex.	Wing.	Tarsus	Tail	Toe.	Culmen
A.22079	A.A.E.	Cape Denison	26.11.13	♂	154	33	69	27.5	13
A.30228	"	" "	? 12.13	♂	153	32	66	27	12
A.30230	"	" "	"	♂	159	34	74	28	13
MM.R5997	"	" "	"	♂	150	33	65	27	12.5
MM.R5998	"	" "	"	♂	155	33	69	27.5	13
MM.R5999	"	" "	"	♂	156	35	70	27	13
MM.R6000	"	" "	"	♂	146	32	63	25.5	11
MM.R6001	"	" "	"	♂	148	32.5	63	27	11.5
MM.R6002	"	" "	"	♂	158	34	68	26.5	12.5
MM.R6003	"	Mackellar Islands	"	♂	155	32	70	26	13
MM.R6004	"	" "	"	♂	153	33	71	27.5	12
BANZARE.1234	R. A. Falla	Cape Denison	5. 1.31	♂	155	35.5	66	27	13
BANZARE.1235	"	" "	"	♂	152	34	72	28.5	13

SOUTH SHETLANDS AND GRAHAM LAND PENINSULA

Number.	Collector.	Locality.	Date.	Sex.	Wing.	Tarsus	Tail	Toe.	Culmen
AMNH	A. G. Bennett	Deception Island	23.12.21	♂	151	33	68.5	27	12
"	"	Wilhelmina Bay	8. 2.22	♂	147	34	67.5	27.5	13
"	"	Deception Island	9. 3.22	♂	156	34.5	69	28	12.5
"	"	" "	"	♂	150	35	66	27.5	13
"	"	" "	"	♂	154	35	71	28	12
"	"	" "	3. 1.22	♂	151	35	73	27.5	12.5
BM.44.1.18.159	Ant. Expedition	Off Louis Philippe Peninsula	2.1.1843	♂	154	35	71.5	28	12
BM.44.1.18.31	"	" "	27.1.1843	♂	147	34	64.5	29	12
BM.1925.10.4.26	A. G. Bennett	Deception Island	8. 2.14	♂	155	34	66	27	12.5
BM.1924.5.8.29	J. E. Hamilton	" "	1. 1.21	♂	155	34.5	69.5	29	12
BM.1924.5.8.28	"	" "	"	♂	155	34	74	29.5	12
BM.1933.10.16.2	"	" "	28.11.20	♂	155	34	71.5	29	—
BM.1933.10.16.1	"	" "	"	♂	142	36	71	27.5	12.5
BGLE.199	B. B. Roberts	Argentine Islands	10.12.35	♂	154	35	63	30	12
BGLE.208	"	" "	13.12.35	♂	149	32.5	73	29	13
BGLE.116	"	" "	24. 2.35	♂	144	31.5	61	27.5	13
BGLE.114	"	" "	"	♂	159	34.5	69	28.5	13
BGLE.113	"	" "	"	♂	156	34	73.5	28	13
BGLE.95	"	" "	30. 1.35	♂	155	34	65	28.5	12
BGLE.209	"	" "	13.12.35	♂	155	34.5	69	29	12
BGLE.112	"	Port Lockroy	11. 2.34	♂	149	33	68.5	27	12
BGLE.84	"	" "	23. 1.35	♂	154	35	74	29.5	12.5
BGLE.96	"	" "	9. 2.35	♂	154	35	72	27.5	12
BGLE.206	"	Argentine Islands	12.12.35	♂	148	36.5	69	29	12.5
BGLE.584	"	" "	11. 2.37	♂	154	34	69	30.5	12.5
BGLE.585	"	" "	"	♂	148	32	67	29	12
BGLE.586	"	" "	"	♂	156	34	73	30	12
BGLE.593	"	" "	"	♂	151	34	70	31	11
BGLE.594	"	" "	"	♂	150	35.5	70	31	11.5
BGLE.596	"	" "	"	♂	156	34	69	28	12.5
BGLE.598	"	" "	"	♂	160	35	72	29.5	11.5
BGLE.600	"	" "	"	♂	157	32	70	27	12.5
BGLE.648	"	" "	2. 1.35	♂	152	33.5	72	28.5	13

For measurements of the specimens in the American Museum of Natural History, I am indebted to Dr. R. C. Murphy who kindly remeasured the wings in the flat position instead of the chord, as published previously, so that all would be directly comparable. The measurements from birds in the museums at Sydney, Melbourne, and Auckland, have been taken from Falla's report (1937). The remainder were made by the author.

Statistical treatment of the longest series from one locality (16 ♂ and 15 ♀ from Graham Land) shows that the chance of there being any significant difference in size between the two sexes is less than 1 in a 100. In the following discussion the measurements of both sexes have therefore been treated together.

The measurements are shown graphically in fig. 2. Those of tarsus and toe exhibit little variation, but the wing and tail measurements tend to be markedly smaller in the birds from lower latitudes. The maximum, minimum and mean measurements for wing and tail are listed in Table II. No precise significance can be attached to

TABLE II
OCEANITES OCEANICUS
MEAN, MINIMUM AND MAXIMUM MEASUREMENTS

Locality.	<i>S. Shetlands and Graham Land</i>	<i>Queen Mary Land and MacRobertson Land</i>	<i>Adélie Land</i>	<i>South Victoria Land</i>	<i>South Georgia</i>	<i>Kerguelen Islands</i>	<i>Falkland Islands</i>	<i>South America</i>
<i>No. of Specimens.</i>	33	15	13	11	14	10	6	11
<i>Measurements.</i>	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Length of wing:								
Mean	152.5±0.7	154.1±1.3	153.4±1.0	155.2±1.1	148.5±0.8	144.5±1.0	136.8±1.7	139.4±0.8
Minimum	142	142	146	149	144	139	132	136
Maximum	160	164	159	159	154	150	142	143
Length of tail:								
Mean	69.5±0.5	69.1±0.8	68.0±0.9	71.7±0.9	63.0±0.6	59.3±0.4	62.6±1.4	58.0±0.8
Minimum	61	63	63	66	60	57	56	54.5
Maximum	74	75	74	75	68	62	65	63.4

the means, stated alone, since the variations in the individual specimens are known to be considerable. It does not follow that the same values would be obtained if further series of the same number of specimens be taken at random from the same localities. It has therefore seemed useful to include in Table II the standard error of each mean. This is written after the mean with the sign \pm and it shows the order of dispersion of the various measurements, or the reliability of the mean.

Comparison of skins from each locality shows no variation in plumage which is limited to any one locality or group of localities. Since there is also an overlap in extreme measurements from the different localities, it is impossible to determine with absolute certainty the origin of any single unlabelled specimen of *Oceanites*. For this reason some ornithologists would doubtless prefer to "lump" them all together and

abandon the use of trinomials. We can, however, determine whether the measurements provide sufficient data to show significant differences in size between the *populations* from the different regions, the test of significance being based on a comparison between the dispersion in the individual populations, the differences between their means, and the number of observations. The figures have been treated in accordance with the rules given by Bannister (*Elementary Applications of Statistical Method*, London, 1939). Bannister (p. 43) takes the number of observations to be the total number of observations in both samples. In the present case, the sizes of the samples are so different that it has seemed better to take instead the number of observations in the smaller sample of each pair. The effect of this has been to create a more severe test of significance. In two populations which are here classed as significantly different the chances of this being reality are therefore much greater than the figure of 100 to 1 given by Bannister.

Each pair of means for the eight regions under discussion has been compared in turn. Using the results for wing measurements, the samples fall into three natural groups of which the respective members are not significantly different from each other, but are all significantly different from those in the other two groups.

I. Graham Land, South Shetlands, Queen Mary Land, Adélie Land, and South Victoria Land.

II. South Georgia and Kerguelen Islands.

III. Falkland Islands and Tierra del Fuego.

If the same calculations are made with the tail measurements : group I remains the same, South Georgia and Kerguelen are significantly different from each other as well as from all the others, and Tierra del Fuego is significantly different from all except Kerguelen. Probably the Falkland Island measurements are significantly different from several of the others, but the number of specimens is really too small to allow fair mathematical treatment of the figures.

The wing lengths show the greatest differentiation and these become progressively longer as higher latitudes are reached. It is noteworthy that the climate of both South Georgia and Kerguelen is in many respects polar rather than sub-Antarctic, while that of the Falkland Islands and Tierra del Fuego is definitely sub-Antarctic. Until further specimens are collected, it seems most convenient to regard the birds as four subspecies. The three groups mentioned above are separable on wing length, and those in group II (from Kerguelen and South Georgia) are separable from each other by the lengths of their tails.

NOMENCLATURE

The following subspecific forms have previously been described:

(1) *Oceanites oceanicus oceanicus* (Kuhl)

Procellaria oceanica Kuhl: Beitr. Zool. 1820, p. 136, pl. 10, fig. 1. No type locality given by Kuhl. South Georgia designated as a nesting station by Murphy, Bull. Amer. Mus. Nat. Hist. XXXVIII, 1918, p. 128.

Mathews: Birds of Australia, Vol. II, Part I, 30 May 1912, p. 13, restricted the type locality. He says: "No locality is given for the specimen, but inasmuch as Kuhl accepted Banks's (that is, Solander's) name and Parkinson's drawing as representing his species, we may accept the locality of that specimen, namely the South Atlantic Ocean, off the mouth of the Rio de la Plata, as the type locality of Kuhl's *Procellaria oceanica*."

Dr. G. C. A. Junge has kindly made a search for the type specimen among Temminck's collection in the Rijksmuseum van Natuurlijke Historie at Leiden, but it cannot be traced. Without measurements, the breeding locality of this bird cannot be determined, and I have thought it best to use the name *oceanicus* for the form breeding at South Georgia. The type locality must remain as South Atlantic Ocean, off the mouth of the Rio de la Plata, but as Wilson's Petrel obviously does not breed in that locality its designation was most unfortunate.

(2) *Oceanites oceanicus exasperatus* Mathews

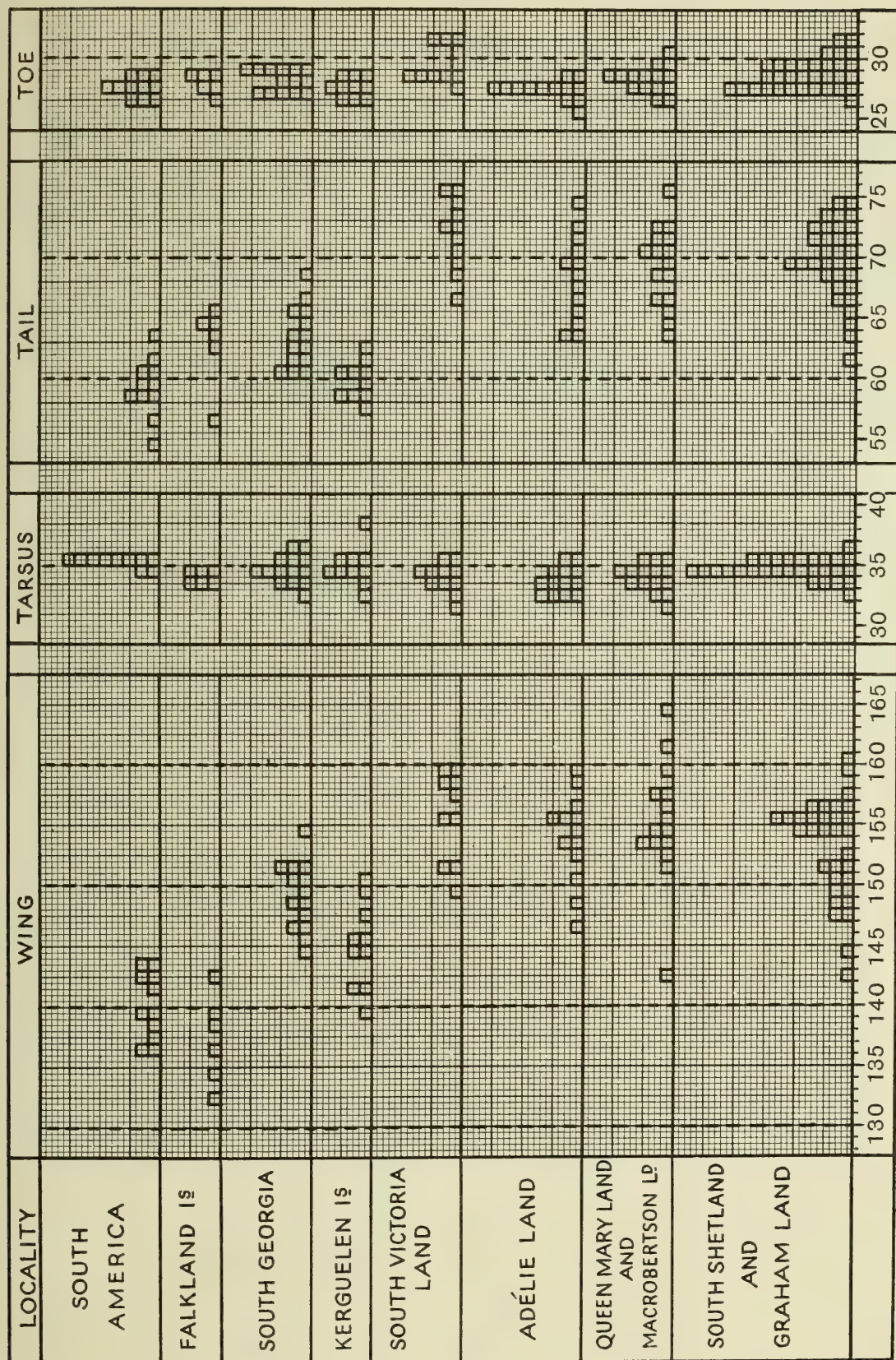
Mathews: Birds of Australia. Vol. II, Part I, 30 May, 1912, p. 11, pl. 68. Type locality "New Zealand Seas". The type is a ♂ in the Rothschild Collection, now in the American Museum of Natural History. It was obtained as a frozen specimen in the London market on 2 March 1905, and was supposed to have come from "Islands south of New Zealand". Mathews (*loc. cit.*) wrote: "I have so named it as examination of series of South Atlantic ocean specimens in comparison with South Pacific ones shows that the latter are larger in all their measurements."

Dr. Murphy has sent me the following measurements for this specimen: wing 155, tarsus 35, toe 27·8, tail 69·3, culmen 12·7. From fig. 2 it is clear that this falls within the limits of Group I, and *exasperatus* therefore stands for the birds breeding on the Antarctic Continent. Since Mathews gives the type locality as New Zealand Seas, it is not possible to restrict this to somewhere outside what could be taken as included in that term, but the measurements are obviously of an Antarctic breeding bird.

(3) *Oceanites oceanicus chilensis* Murphy

Murphy: Oceanic Birds of South America. 1936, Vol. II, pp. 754–757. Type—No. 3316, ♂, in Brewster Sandford Coll., Amer. Mus. Nat. Hist.; Wollaston Island, Chile. Collected on 1 January 1915 by R. H. Beck. Murphy gave the average measurements of 11 birds collected on or near the breeding grounds at Wollaston and Morton Islands, Nassau Bay, and at Magellanes in the Strait of Magellan, and of 40 others taken during migration at various points on the west coast of South America. He concluded that, although extreme measurements overlap, *chilensis* is consistently smaller than the typical race in the lengths of wing, tail and culmen.

The name *chilensis* was first published by Alexander (1928), but Murphy (*loc. cit.*) explained this prior use. It is not citable from Alexander, since the name is a *nomen nudum* at that point. Unfortunately it was also quoted as a synonym of *oceanicus* by Mathews (1934), and so cannot be allowed to stand. In a more recent paper, Mathews (1937) gave *wollastoni* as an "alternative name" for *chilensis*, but this also is a *nomen nudum* and, being quoted as such under *O. o. chilensis*, cannot be used. There is thus no name available for the form which breeds in Tierra del Fuego.

FIG. 2.—Measurements of *Oceanites oceanicus* in mm.

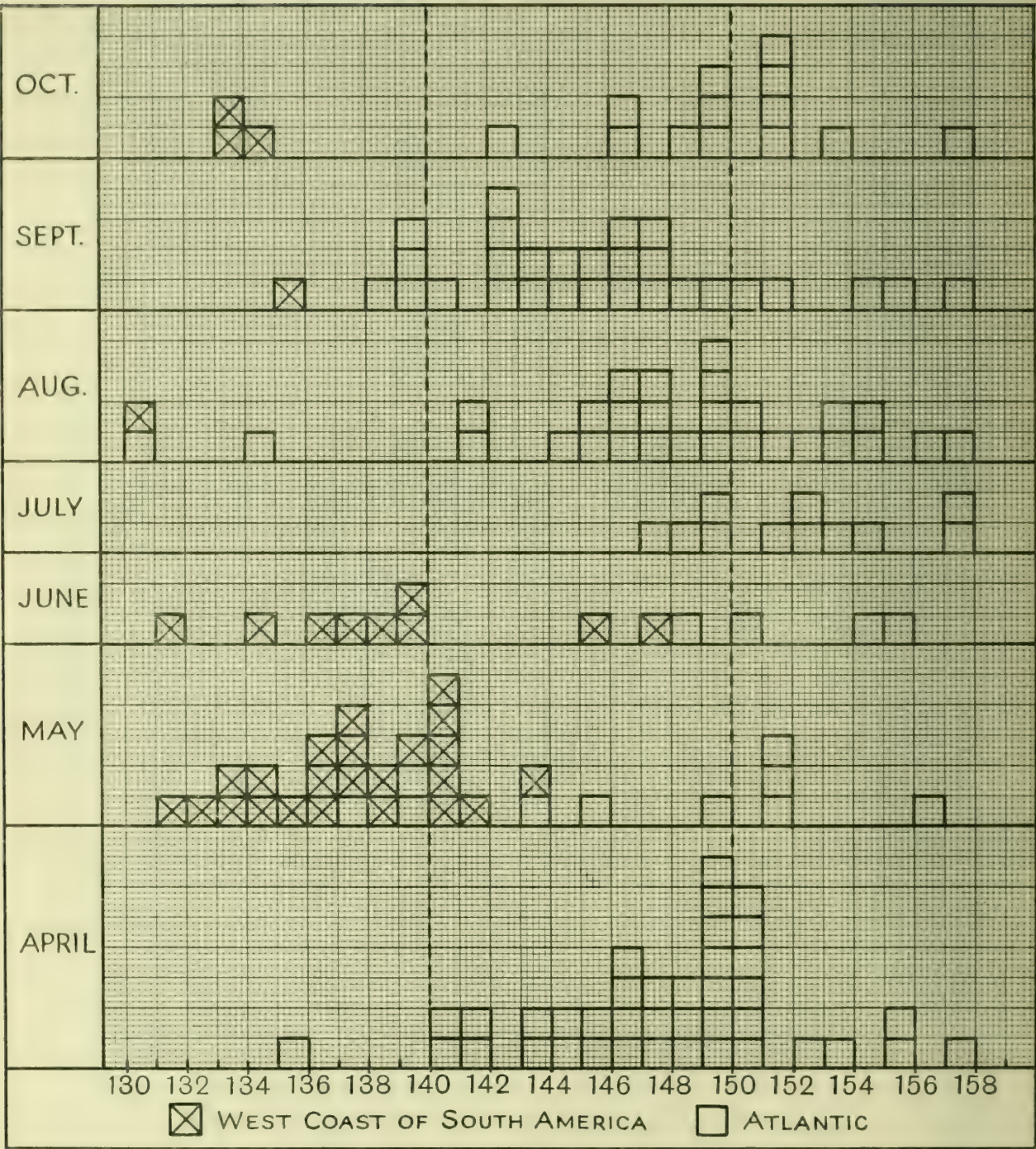


FIG. 3.—Wing measurements of migrating *Oceanites oceanicus* in mm.

Dr. Murphy has requested me to give the bird a legitimate name, and I therefore propose: *Oceanites oceanicus magellanicus* nom. nov.

(4) *Oceanites oceanicus parvus* Falla

Falla: B.A.N.Z.A.R.E. Reports, Series B. Vol. II, 20 August 1937, p. 208. Type—No. 1073, ♂, in the B.A.N.Z.A.R.E. Collection from Royal Sound, Kerguelen, 10 February 1930. Falla gave the average measurements of seven Kerguelen breeding birds which he described as differing from the typical form in their smaller dimensions and less defined pale edging on the greater wing coverts. However, he suggested that this new subspecies might possibly be identical with *O. o. chilensis* Murphy of which he had no specimens for comparison.

The pale edging of the greater wing coverts is a very variable character which occurs to a greater or less extent in specimens from nearly all the breeding localities (see p. 188). In the British Museum there is only one breeding specimen from Kerguelen and one from South America: both males. Comparison of these shows no plumage difference which could justify separation of the birds from these two localities. Both have slight pale edgings to the greater wing coverts. In the same way there is no significant visible difference between the South American bird and those from the Falklands. There is, however, a tendency for South American specimens to have very small bills. The name *parvus* is available for the birds breeding at the Kerguelen Islands.

To summarize: we have four populations differing only in the mean of their measurements. To these four populations it is convenient to give subspecific status. Their correct names and synonymy are listed below with their breeding localities:

(1) *OCEANITES OCEANICUS OCEANICUS* (Kuhl)

Procellaria oceanica Kuhl, Beitr. Zool. Vergl. Anat., Zweite Abt., p. 136, 1820.

(?) *Procellaria Wilsonii* Bonaparte, Journ. Acad. Nat. Sci. Philad., Vol. III, p. 231, pl. ix. 1824.
South Georgia.

(2) *OCEANITES OCEANICUS EXASPERATUS* Mathews

Oceanites oceanicus exasperatus Mathews, Birds Austr. Vol. II, part I, p. 11. 1912.

Graham Land, South Shetlands, Queen Mary Land, Adélie Land, South Victoria Land.

(3) *OCEANITES OCEANICUS PARVUS* Falla

Oceanites oceanicus parvus Falla, B.A.N.Z.A.R.E. Reports. Series B, Vol. II, p. 208. 1937.
Kerguelen Islands.

(4) *OCEANITES OCEANICUS MAGELLANICUS* Roberts.

Oceanites oceanicus chilensis Murphy, Oceanic Birds of South America, Vol. II, pp. 754–57. 1936 (*nomen nudum*).

Oceanites oceanicus wollastoni Mathews, Emu, Vol. XXXVII, p. 141.
1937 (*nomen nudum*).
Falkland Islands, Tierra del Fuego.

THE IDENTITY OF BIRDS CAPTURED DURING MIGRATION

As already noted, the identity of individual *migrating* birds cannot be determined with absolute certainty. In fig. 3 the wing lengths of migrating birds have been plotted opposite the months in which they were captured. It should be remembered that some, at least, of the small measurements are due to abrasion of the wing tip or moulting of the longest primary, but only those birds which appear, from their bills, to be fully adult have been included. Those taken on the west coast of South America are shown with a different notation from those taken in the Atlantic. It will be seen that there is a strong tendency for the smaller specimens to occur on the Pacific coast and this suggests that the majority of the birds from Tierra del Fuego migrate up the Peru Coastal Current, while those from West Graham Land keep to the Atlantic. Probably most of the small birds in the Atlantic come from the Falkland Islands. The Peruvian coastal birds are slightly shorter winged than most of the breeding birds from the Magellanic region.

It must be admitted that owing to the overlapping of measurements, the division into four races may not be useful for museum purposes. Unlabelled specimens or migrants cannot be allocated to a particular race with confidence, but it would seem that separate names are required to draw attention to the differences in the populations from the different breeding localities. It is suggested that a binomial only should be used to describe migrant birds captured at sea, but the subspecies concept appears to remain serviceable in a case like *Oceanites* where the birds breed on isolated islands.

DESCRIPTION OF ADULT MALE AND FEMALE FROM GRAHAM LAND¹

Upper parts "fuscous black", lores, chin and upper throat "fuscous"; in some birds a few partly white concealed feathers immediately in front of the eye; greater wing-coverts paling off to "cinnamon drab"; all upper-tail-coverts entirely white, but feathers of lower rump "fuscous" with white tips; lateral under tail-coverts with varying amount of white, tail black, shafts of the lateral retrices towards the base, and the portion of the inner web adjoining, white; under wing-coverts "benzo brown"; lower scapulars "fuscous black" with paler tips; large white patches on lower flanks; white at base of retrices confined to inner webs and shaft extending as a streak for about two-thirds of length on outer pair; when fresh, the feathers of the belly have very faint white tips; primaries black with edges of inner webs "fuscous black"; bill, tarsus, toes and claws black; inner portion of the webs between the toes "maize yellow", sometimes marked with irregular dark blotches; iris dark brown.

Before each moult, the whole plumage fades to a slightly lighter colour, and many of the white feather tips are worn off. This fading is most marked on the greater wing coverts which show up more distinctly as conspicuous pale bands across the wings.

¹ Colours from Ridgeway's *Colour Standards and Nomenclature*. Washington, 1912.

THE COLONY AT THE ARGENTINE ISLANDS

The northern base of the British Graham Land Expedition was in the Argentine Islands (Lat. $65^{\circ} 15' S.$, Long. $64^{\circ} 15' W.$). This group comprises a number of small rocky islets, many of which become partly free of snow in summer. In places there were quite large patches of moss which had formed a "peat" as much as 3 ft. in thickness. These patches of moss were normally, but not invariably, areas which had a northerly aspect and remained continuously well blanketed by snow during the winter. Flourishing moss areas of this type were found at other points along the coast, but only on a certain type of well-sheltered inshore island, for the lower slopes of the mainland are too heavily encumbered with ice, whilst islands that are low or more exposed are liable to frequent drenching with salt spray.

The discovery that Wilson's Petrels were nesting in many of these moss patches opened up possibilities of observation which would have been quite out of the question in the more usual sites under boulders or in screes. No less than seven colonies of Wilson's Petrels were found in the Argentine Islands, and four of these were in moss patches. The most accessible—situated on the west side of Galindez Island about 400 yards from the base hut—was selected for regular observation; while the other colonies provided specimens and were used for experiments which were likely to cause disturbance.

Most of my observations on breeding habits were thus made in a single colony consisting of 23 nests. The burrows were in a small north-facing moss patch about 20 ft. above the sea, and all were within a narrow strip of about 9 yds. along the edge of the cliff. The method of observing was to cut very carefully a cylindrical portion of hard, compacted moss from immediately above each nest cavity. This piece of moss had a numbered wooden peg, driven through it, and served as a very convenient "lid" which could be lifted for the purpose of inspecting the nest at any time (plate III, fig. 2). The colony was visited every day and notes made at each burrow. Observations on the growth of the chicks were made in 1935 between 13 February, when we arrived at the Argentine Islands, and the end of April, when the birds migrated north. In the Spring of 1935-36 there was opportunity to study their return from migration, their courtship, and the various activities connected with incubation. These observations were interrupted on 2 January 1936, owing to my departure on a summer cruise, but were resumed on 29 January, before any of the eggs had hatched. On 16 February 1936, the Expedition left the Argentine Islands to establish a new base farther south, but before we left, the Wilson's Petrel chicks had reached the same stage of growth as on our first arrival the year before. The complete breeding cycle was thus covered. In these two seasons most of the birds in the colony were marked with small numbered aluminium rings. Another visit was made in February 1937, and it was then possible to check the earlier conclusion that each bird returns annually to the same burrow and mate. Since it was necessary to determine the sex of all the birds under observation, it was unfortunately necessary to conclude the observations by dissecting one bird from each of the marked pairs.

There were considerable difficulties in making the observations at regular times. To reach the colony meant rowing up the creek from the base hut and landing on another island. Sometimes the weather was so bad that this short row took as much

as an hour. When the creek was blocked with loose ice a boat could not penetrate through the floes, so a rope bridge had to be built across the narrowest part of the channel and the only route to the colony was by a long walk through deep soft snow. Sometimes, too, the cliff at the colony was so slippery with ice that some of the more inaccessible burrows were not examined. The recorded times are all L.M.T. 4 hours slow of Greenwich. Rough pencil notes were made at the colony and afterwards written up in greater detail in the warmth of the hut. From these notes it has been possible to make generalized statements about the usual events which go to make up the behaviour pattern of the species, but careful examination of the various tables, which summarize the observations, show some inconsistencies. Some, but not all, of these inconsistencies are probably due to interference.

THE BURROW

The most usual nesting site is in a cavity under loose pieces of rock, sometimes a long way in and quite inaccessible; but where there is any soil the birds are often found in burrows. On Kerguelen Island, Hall (1900) says that the nests are often made of small stalks, principally of *Azorella*, in shallow indentations beneath stones or in any suitable chinks or crevices in slopes of shattered rock. He adds that the egg is usually laid on the bare ground in a shallow depression. In the Cape Horn area, Reynolds (1935) found them nesting in burrows or natural holes in damp peaty soil with a covering of *Azorella* and *Empetrum*. In the South Orkneys, Ardley (1936) excavated six nests "actually made in blocks of ice which had evidently formed among the rocks during the winter". Wilson's MS. notes (1901) describe a burrow at Cape Adare in which the floor of the tunnel was smooth ice and the nest cavity was lined with feathers of the Adélie Penguin (*Pucheranphus adéliae*). Hunter (in Falla, 1937) found nests on Macquarie Island which were also formed largely of penguin's feathers.

In the Graham Land peninsula and South Shetland Islands, it was common to find nests among shattered rocks, but as already described, they were also discovered in sloping moss patches where the soil enabled the birds to use burrows. These burrows usually led in horizontally from the bottoms of small cavities between the bright green moss hummocks. Many of the nests were in natural moss cavities, but the majority could only have been excavated by the birds themselves. These burrows averaged about 40 cms. long and had a diameter of 10 to 15 cms. at the entrance. The inner end opened out into a small chamber containing the nest—a shallow depression in a collection of small moss root fragments. The nests were usually very dry, in contrast to the damp tunnels leading to them. The same burrows are used year after year; new material being placed on top of the old nest. In one burrow I found the remains of egg-shells indicating the presence of five past nests under the existing one. Sometimes, in situations far from any vegetation, there was no attempt to build a nest, and the egg had been laid on the bare ground, but it was rare to find nests in which absolutely no material had been collected.

ARRIVAL, COURTSHIP AND MATING

Fig. 4 summarizes what is known of the dates of arrival, egg-laying and departure in various breeding localities. These records will be discussed again under

"Migration", but for the present it is enough to point out that the dates of arrival at each locality seem to be remarkably constant. They also show that a period of 3 to 4 weeks elapses between the date of arrival and the appearance of the first eggs.

At the Argentine Islands in 1935 the first Wilson's Petrel was seen on 24 November, about a week after the colony had become clear of snow. After this date, birds were seen flying round the islands every evening, but apparently they do not visit their burrows immediately on arrival. The visits of the adults were checked by the same method as that used by Lockley (1930). A light lattice of a stiff, feathery lichen (*Usnea* sp.), set up across the entrance of the burrows, was easily brushed aside

Locality.	First seen.	Egg dates.	Last seen.	Authority.	Notes.
McMurdo Sound	Mid.-Dec. 1903 and 1904	—	End of Feb. 1903 and 1904	Wilson	—
Cape Adare	—	9 Jan., 1902	—	"	—
Cape Denison	4 Nov., bulk early in Dec. 1912	—	7 Mar. 1913	Falla	—
"	5 Nov., 1913	13 Dec., 1913*	—	"	—
Mackellar Is.	—	18 Dec., 1913	—	"	—
Kerguelen Is.	First week Dec. 1874	23 Jan., 1875	—	Eaton	—
"	Third week Nov 1874	22 Jan.*	—	Sharpe	Fresh eggs found in Feb.
"	8 Dec., 1874	—	—	Coues & Kidder	—
"	Mid. Dec. 1913	24 Jan., 1914	—	Loranchet	First chick found 22 Feb.
"	—	3 Feb., 1897*	—	Hall	Hard set eggs also found on 3 Feb.
South Orkneys	—	4 Jan., 1933	—	Ardley	Ditto on 4 Jan.
"	11 Nov., 1903	11 Dec., 1903*	23 March, 1904	Eagle Clarke	No chicks hatched by 21 Feb., 1904
"	12 Nov., 1904	—	—	"	—
"	—	End of Dec. 1904	—	Valette	—
S. Georgia	Nov.	Early Dec.	May	Matthews	—
"	—	—	End of March 1905	Lönnberg	—
Paulet I.	7 Nov., 1901	—	—	Andersson	—
Snow Hill I.	—	—	24 March, 1902	"	—
Hope Bay	—	31 Jan., 1905	—	"	—
Andvord Bay	9 Nov., 1921	—	2 April, 1921	Bagshawe	—
Deception Is.	—	11 Jan., 1936	—	Roberts	—
Wandel I.	—	13 Dec., 1904*	—	Ménégaux	—
Petermann I.	23 Nov., 1909	10 Jan., 1909	22 April, 1909	Gain	First chick found 16 Feb., 1909
Argentine Is.	24 Nov., 1935	17 Dec., 1935*	3 May, 1935	Roberts	—
Debenham Is.	13 Dec., 1936	—	2 April, 1936	"	—
Deceit Is.,	—	14 Dec., 1932*	—	Reynolds	—
Cape Horn	—	—	—	—	—
Wollaston Is.,	—	1 Jan., 1915	—	Murphy	—
Cape Horn	—	—	—	—	—

* First dates on which *fresh* eggs were found.

FIG. 4.—Dates of Arrival and Departure from Breeding Localities and Egg-dates.

by birds entering or departing. Thirteen burrows were blocked in this way, and it was not until the night of 1–2 December that any of these lattices were disturbed.

During these first days a few birds came in from the sea at about 19.00 hours each evening and flew round the colony for about an hour. It was rare to see more than two at a time. After 2 December the burrows were visited during the night at irregular intervals, and sometimes one or both birds remained during the day. After 10 December it was not uncommon to find a pair together, but more often single birds, of either sex, were found in the nest during the day.

My observations at the prepared burrows have been summarized in fig. 5. They were not as complete as I should have liked, but anyone who has attempted similar work will appreciate the reasons. They do, however, show clearly the very irregular visits made to each burrow before the egg is laid.

Wilson's Petrels were seldom seen flying round the colony during the day. They came in from the sea each evening and flew up and down above the colony. This night-flying is very similar to that of Leach's Petrel and it undoubtedly forms an important part of their courtship activities. A visitor to the colony in the half-light at midnight would see 15 to 20 birds flying up and down the cliff-face, closely following the inequalities of the rocks and then circling round like Swifts (*Apus apus*) over the sea-ice in the bay. Every few minutes one would alight for a short time before resuming this flitting up and down. Sometimes a bird would enter a burrow, but more usually they remained sitting outside. If one bird of a pair was inside, it was common for its mate to alight repeatedly at the entrance and utter its chattering call, which would be answered immediately. Frequently, one would chase another—both following the same zigzag course at great speed. At these times the white bar at the base of the tail is strikingly conspicuous. Possibly it acts as a "releaser"¹ eliciting a flying-in-pursuit reaction.

As the birds circled past the cliff-face, they nearly always paused opposite the entrance to their nests. They might alight three or four times before finally going inside. Once on the ground they are surprisingly active, running along flat or even vertical surfaces with the greatest ease. They land very lightly on the whole length of the tarsus, and can do this without difficulty on quite sharply projecting rocks. They can and do stand upright for very short periods, but usually they move along on half-bent tarsi, with wings closed or fluttering to sustain some of their weight. When on the ground, the great length of the tibia (see plate VII) keeps them well off the surface so that even with the tarsus horizontal only the tip of the tail touches the ground. They have no difficulty in taking off—springing into the air with the legs.

In the descriptions of courtship which follow, it should be clearly understood that there is no question of selecting a mate. Use of the word "courtship" does not imply doubt as to the outcome, and it would seem that in this case its function is mainly that of mutual stimulation.² Ringing results show conclusively that the adults return year after year to the same burrow and to the same mate. Three birds ringed in March 1935 returned to the same burrows the following December. In

¹ A term proposed by Lorenz (*Auk*, LIV, 1937, pp. 245–273) to indicate devices for the production of stimuli which serve as "keys" to "unlock" or release "innate perceptual patterns", and which result in instinctive reactions.

² The testes of a male in full breeding condition are approximately spherical and about 2 mm. in diameter. When they first arrive at the colony the testes are noticeably smaller than this.

December 1935, 27 birds in the Galindez Island colony were ringed, and 22 of these were recovered in February 1937. All of these re-occupied their old burrows, and 20 had the same mate again. The other two belonged to pairs of which only one had been marked, while all but one of the 5 birds which were not recovered had occupied burrows which were badly damaged by sledge-dogs. Their absence was therefore not surprising.

Nst N.	Date.	Dec.																															Jan.	
		2	4	6	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2				
	Time of observation.	?	?	1200	?	?	?	?	1500	1500	1200 2200	1500	1500	1800 2200	1500	1500	1400	1400	1500	1500	1500	1800	1500	1400	1400	1400	1100	1500	1500	1500	1400			
						2																												
2		0-0	0*						.	0 0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1●	1				
3															2	0	0-	0-	0-	0-	0-	0-	0-	0*	0*	1	0*	0	0*					
7						-	*	2	0	0-	0-	0-	0-	0*	0*	0*	0*	0-	0*	0*	1●	1	0	1	1	1	1	1	1	1	1	1		
8		0-	0-	1	-	-	0-	0-	0*	1	0 2	0	0-	0*	0-	0*	0-	0*	0*	0-	0*	1●	2	1	0	2	1	1	1	1	1	1		
9		0*	0*	0*	0-	0-	1	0	0	2	0 0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0		
9		0-	0*	0*	0	0	0	0	0	0	0 0	1	0	0 0	0	0*	0*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
1		0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0*	2	0	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0-	0*	.		
2		-	0*	0*	0-	0-	0-	0-	0-	0	0 1	0	0-	0-	0-	0*	0	0	0	0	0	0	0	0	2	0*	0	0	0	0	0	0		
5		0*												0 1	0	0-	0*	0*	0	0														
6						1	1	0	0	0	0	0	0	0 1	0	0	0	0	1	0	2		0	2		0	0							
7		0-	0-	0-	0-	0-	0-	2	0	0 0	0	0	0 0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0		
8										0 2	0	0	0 0●																					
20																0*	0	0	0	0	0	1	0●	1	1	1	1	1	1	1	1	1		
24						2																												

Symbols:

1 = 1 bird in burrow at time of observation.

2 = 2 birds " " " "

0 = no " " " "

● = egg laid since last observation.

* = nest visited since last observation.

- = nest not visited since last observation.

. = repairs or additions to nest visible.

Observations were made twice on 14 and 17 December. A space indicates that the nest was not examined.

FIG. 5.—Observations during Courtship Period

Several other points emerged from this ringing. Two pairs which deserted their burrows owing to interference in 1936 returned to the same burrows in 1937. In all the records there is only one case of a bird being found in the wrong burrow. It seems probable that it is the joint "ownership" of a nest rather than any mutual bond between individuals which brings the pairs together again each year. I believe that they first meet in the burrow at the beginning of each breeding season, but it is possibly significant that the association of two birds at sea was often noted. No conclusive evidence was obtained as to the age at which young birds first breed, but since no marked chick was recovered, it is suggested that they probably do not breed until they are at least 2 years old.

In order to obtain a clearer picture of their courtship activities, the comings and goings of a single pair were automatically recorded with a 2-bulb thermograph. One bulb gave a record of the air (shade) temperature outside, while the other was arranged in the burrow so that the trace on the chart showed a slight oscillation when a bird was inside and gave a perfectly smooth trace when no bird was present. The records were not entirely satisfactory, but since the birds had to sit actually on the bulb while in the nest cavity, active courtship of two birds gave a recognizable oscillation on the chart. Their visits were also checked by blocking the entrance in the way already described, and comparison of the two traces helped to eliminate errors due to sudden fluctuations in air temperature.

It was not always possible to tell with certainty whether one or two birds were in the burrow. The visits are shown in fig. 6 in which the presence of two birds is indicated only when this was checked by direct observation. It is certain that no bird remained in the nest cavity during the intervals represented in the figure, but it is possible that there may be *small* errors in time. Events can be reconstructed as follows: At midday on 6 December a single bird was found in the nest for the first time. It left in the evening and the burrow was not visited again until the 11th. That night two birds were in together from 21.00 hours until about midnight. At about 22.00 hours on the 12th a single bird entered and remained all the next day. It was joined by its mate at about 22.00 hours on the 13th, and both remained in together until about 16.00 hours on the 14th. The nest was not visited at all on the 15th. A very brief visit was made at about 20.00 hours on the night of the 16th, and early on the night of the 17th a bird was in, but the time record was indistinct. Between the 17th and 24th the burrow was only visited on four nights. The egg was laid during the night of the 24th, and thereafter one or other of the birds remained incubating.

I was unable to find any correlation between the times of these visits and weather conditions. The only occasion during this period when both were in together for any length of time was on the 13th-14th, but I have no doubt that each night the birds flew up and down over the colony for a considerable time before entering the burrow, and that they also alighted frequently without going inside.

Apart from this night-fighting, courtship activities take place inside the nest cavity. Although copulation was never observed, there can be little doubt that it takes place inside the burrow. It was not possible to watch their activities by torch-light without disturbing them, but in daylight close observations could be made by lying with the face over the observation hole, with a coat thrown over to exclude all

light except that which came through the normal burrow entrance. Under these conditions a pair would behave in an apparently undisturbed manner. There was a regular procedure which was always followed in the same order. The two birds sat side by side in the nest cavity; facing the same way; and alternately preened each other's head feathers, running their bills with a vibrating motion all over each other's heads and occasionally pausing with heads pressed together. They would change actions every few seconds; first one doing the preening, then the other. After about 2 minutes of this behaviour one would firmly grasp the bill of the other in its mandibles and do a quick vibrating movement which was very difficult to follow.

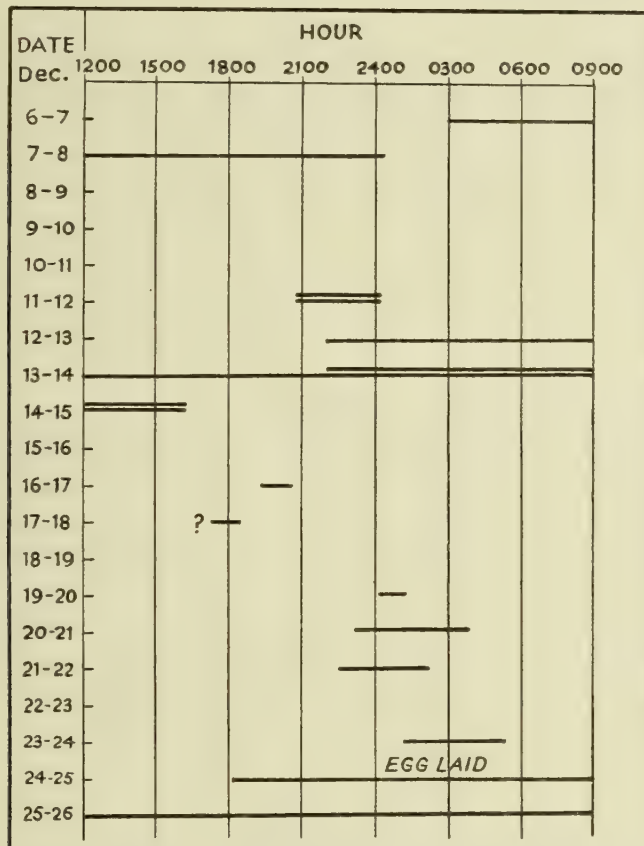


FIG. 6.—Visits of Adults to nest 8 during courtship. The horizontal lines indicate the periods during which a bird was in the nest cavity. A double line indicates the presence of two birds.

During this action only—and it invariably happened—both birds would utter their harsh chattering call two or three times. Then both would sit quietly for a while before repeating the whole performance. Their courtship is essentially mutual, with no hint of prior initiative by either of the birds.

Concurrently with these activities, other preparations are made. If the breeding population remains approximately constant, no new burrows have to be excavated. No new ones, in fact, were made in the Galindez Island colony during the three seasons it was under observation. But the old nests were repaired, and several of the burrows were lengthened. Each spring a very definite cup-shaped nest is hollowed

out in the accumulation of dead moss and lichen at the end of the burrow. My barriers of lichen were often carried right inside the burrow and regularly built into the nest each night. Sometimes the nests were enlarged so much in this way that there was hardly room for the birds to get in and I had to remove some material every few days. One pair which had their burrow in a small dome-shaped hummock of moss was evidently too much disturbed by the barrier across the entrance, for in a single night they dug a new tunnel about 6 in. long and leading out of the nest cavity to the opposite side of the hummock. On another occasion, water from a thawing snow patch started to trickle through a burrow. During the night a quantity of moss was carried in to raise the level of the floor above the wet.

Several times I watched soil being thrown out of a burrow entrance, but the actual digging was never observed. Marks show that the feet are used, but adults were noted with earth-covered bills. In order to test their powers of excavation, two adults with chicks were heavily blocked into their burrows with bungs of moss-peat about 4 in. thick. Early next morning both of these had dug their way out through a narrow passage along one side of the bung.¹

THE EGG

Only one egg is laid and this is not replaced if taken. This appears to be characteristic of nearly all the Tubinares. Assuming from this evidence that the ovary only produces one mature egg annually, the birds belonging to this group thereby differ from nearly all other vertebrates. The egg is thin-shelled, elongated oval in shape, dull white, usually peppered with very fine dots of reddish-brown and lilac. These dots usually form a zone near the larger end, but are occasionally sprinkled all over the egg.

The eggs from different localities appear to be indistinguishable. The average of twenty in various collections is 33.4×24.2 mm.; the eggs showing the four extremes measure 36.0×24.0 , 34.0×27.4 , 28.0×23.0 and 32.5×22.5 .

INCUBATION

Incubation starts immediately the egg is laid, and is shared equally by both sexes. Fig. 7 shows typical observations at 6 burrows for 8 days in 1935-36. The symbols indicate the sex of the bird incubating at the time of observation, and the results show that the males and females incubate in alternate spells of approximately 48 hours. Similar observations in 1937 confirmed these results.

In fact, human interference only served to illustrate the fixity of this behaviour pattern. In nest 7, for example, the male was frightened away on his first day of duty (30 December). On 31st no bird was present although the burrow had been visited during the night, and the female did not take over till her normal time on 1 January. In nest 8, however, the incubating bird was disturbed on 28th, and both birds spent the next day in the burrow before resuming their usual alternation.

¹ See p. 167 for remarks on digging through snow-drifts.

Date.	Dec.						Jan.	
	26	27	28	29	30	31	1	2
Time of Observation.	1430	1400	1400	1400	1100	1500	1500	1400
7	♂ *	†	♀	♀	♂ *	†	♀	♀
8	♀	♀	*	♀	♂	♀	♀	♀
10	♂	♂	♀	♀	♂	♂	♀	♀
20	♂	♂	♀	♀	♂	♂	♀	♀
22	♂	♀	♀	♀	♂	♂	♀	♀
23	♂	♂ *	♂	♀	♂	♂	♂	♀

* Bird disturbed and flew out.

† No bird in burrow; egg cold.

The numbers in the left-hand column are those of the nests.

FIG. 7.—Share of the Sexes in Incubation.

Nests 22 and 23 show cases in which each sex incubated for 3 consecutive days, but it is significant that in both nests the egg was subsequently deserted for a day before readjustment to the 2-day alternation.

The change-over always takes place at night, but my records are not sufficiently detailed to show whether this always occurs at the same time. It is certain that the incubating bird is visited by its mate almost every night, whether there is a change-over or not. I only observed the actual change once. After flitting up and down for a time, a relieving bird (a male) alighted at the burrow and went straight inside. As he did so, the incubating bird uttered her chattering call, and was immediately answered. Both birds then called together at short intervals for about 10 minutes, and the female then flew out and went straight out to sea. It was found afterwards that an incubating bird could be made to utter its chattering call by placing a hand in the entrance of the burrow.

The incubation period of 9 eggs was successfully determined. These are tabulated in fig. 8.

Nest Number.	Date of Laying.	Date of Hatching.	Incubation Period.
2	1. 1.36	9.2.36	40 days
7	25.12.35	7.2.36	44
8	25.12.35	11.2.36	48
9	? (after 2.1.36)	?	?
10	20.12.35	30.1.36	41
17	? (after 2.1.36)	12.2.36	?
18	17.12.35	30.1.36	44
19	29.12.35	14.2.36	47
20	25.12.35	2.2.36	39
22	21.12.35	31.1.36	41
23	27.12.35	12.2.36	47

FIG. 8.—Incubation Period.

It will be seen that these nine cases show very marked variation—ranging between 39 and 48 days (average 43 days). The shortest time is probably nearest the true period, as in this case the minimum disturbance was experienced. The variation must be largely due to irregular incubation. Experiments with eggs of the domestic fowl have shown that the period of incubation varies inversely with the temperature at which the eggs are incubated. An increase in temperature leads to accelerated development of the embryo, while a decrease leads to slower development. Direct evidence of temporarily suspended incubation is not lacking in Wilson's Petrel, for it is quite common to find a cold deserted egg, containing a living embryo, in a burrow which has not previously been disturbed. I have no record of such eggs hatching after desertion for more than 48 consecutive hours, but it seems probable that they can survive for much longer periods. In several cases the embryos remained alive when deserted for a whole day just before hatching, at a temperature of only about 1° above freezing.

The temperature in the burrows remains fairly constant and is not subject to the marked diurnal fluctuation of the air temperature outside (see fig. 9). It is noteworthy that the temperature in the burrows does not appear to fall below freezing-point at this time.

It is interesting to compare these observations on the incubation of Wilson's Petrel with those available on two other species of *Hydrobatidae*. With Leach's Petrel (*Oceanodroma leucorhoa*), Gross (1935) found that the two sexes incubated in alternate spells of approximately 96 hours, and that during these periods the mate did not visit the burrow. The longest determined record of continuous sitting was 144 hours. He noted that the egg is often left unincubated for several days, and that 4 eggs kept in the laboratory for 8 days at temperatures of 7° to 29°C . contained living embryos at the end of this time. (The burrow temperature taken at midday ranged between 4.5° and 15.5°C .) On the other hand, Ainslie and Atkinson (1937) noticed no such regularity in the spells of incubation, nor did their observations agree that the mate does not visit the sitting bird. The incubation period of Leach's Petrel has not yet been determined. Gross records that when an egg was broken or removed, it was replaced after 2 weeks; but with Wilson's Petrel I never found a second egg after the first had been taken.

Lockley (1932) determined the incubation period of the British Storm Petrel (*Hydrobates pelagicus*). With 6 eggs the period ranged between 38 and 40 days (average 39.5). In two of these cases he noted that the egg was left cold for one day early in the period. He also records a brief example of the share of the sexes in incubation: "the female sat for 2 days, then the male for 3, then the female for another day, after which the egg was left cold for 2 days, then the male sat for one day, the egg being totally deserted thereafter."

CARE OF YOUNG AND GROWTH OF CHICKS

The dates of hatching which were determined in 1936 are tabulated in fig. 8. In 1937 the exact date of hatching of 12 more chicks was recorded on the following days—all in February: 4th (2), 5th, 8th (2), 9th, 10th (2), 11th, 12th, 13th and 15th.

The egg-shells were usually to be found chipped about 24 hours before the

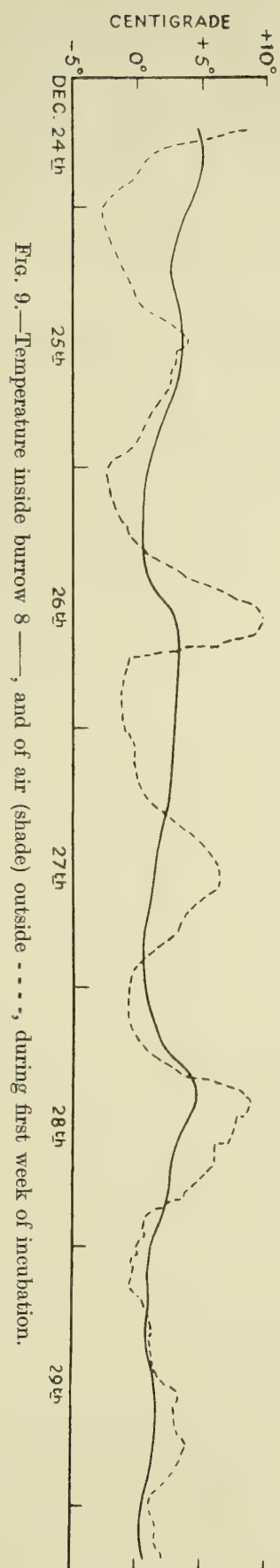


Fig. 9.—Temperature inside burrow 8 —, and of air (shade) outside - - -, during first week of incubation.

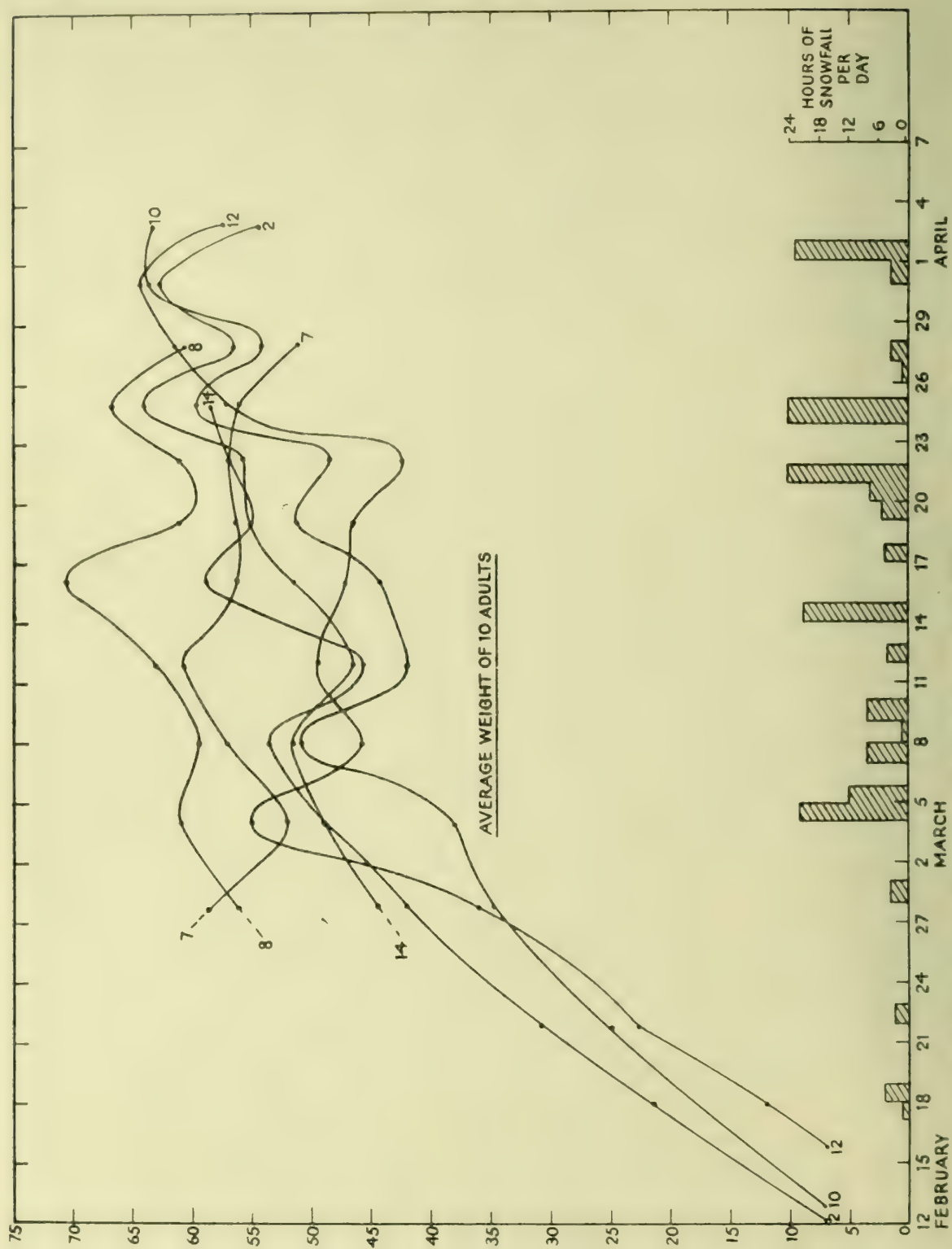


FIG. 10.—Weights of 6 chicks. (Curves drawn in by eye.) The numbers at the beginning and end of each curve are those of the burrows in which the chicks lived.

young birds liberated themselves. The parents did not brood their chicks during the daytime, except for the first day or two after hatching, and after this time the young were always fed during the night.

Owing to various causes which are discussed below, the fledging period is subject to considerable variation.

GROWTH CURVES BY WEIGHT

In 1935, 6 chicks were weighed at intervals throughout their growth. This was done in the shelter of a box with a small balance; the accuracy of the measurements being only to the nearest 0.5 of a gramme. The results have been plotted as growth curves in fig. 10. The exact dates of hatching chicks 2, 10 and 12 were known, whereas 7, 8 and 14 were already some days old when the observations were started. Chicks 10 and 12 were dug out and eaten by sledge-dogs when fully fledged on 3 April. They were then 50 and 47 days old. Chicks 7, 8 and 14 left their burrows on 29 March, 1 April and 27 March respectively. Chick 2 left its burrow on 5 April, and was the only one of which a complete record was obtained. The fledging period of this chick was 52 days.

An examination of the growth curves shows that there is an initial period of steady gain in weight, lasting about 2 weeks, followed by a protracted period of fluctuations. This manner of growth seems to be characteristic of most young altricial birds, and it has been observed in several quite unrelated groups. The fluctuations, however, are more marked than in any other case known to me, and at this stage the average weight of the chicks is considerably more than that of the adults. This weight fluctuation was due to irregular feeding by the parents, which were quite often unable to reach their chicks when the entrances to their burrows were blocked with snow.

LIMITATION BY SNOWFALL

Owing to the differing outlooks of the various burrows, they were not all affected to the same extent. Some were more sheltered from the wind than others and consequently became blocked under deeper drifts. The general correlation between snowfall and loss of weight may be seen in fig. 10 where the number of hours of snowfall each day is plotted on the same graph as the growth curves. It should be noted, however, that the burrows were often blocked by wind-drifting after the snow had stopped falling. My notes show clearly that whenever a burrow was blocked in this way, the weight of the chick decreased; and that as soon as the snow thawed or was blown away, the weight of the chick increased again. There was also some evidence that even if the burrows were not blocked by snow the parents sometimes had difficulty in obtaining foods for their young during periods of bad weather.

Throughout my notes there are constant records of burrows being blocked in this way. When the snow was soft the adults were sometimes able to dig through it to their chicks, but often they gave up after scratching down a few inches. Four typical extracts from my field notes may perhaps make clearer the conditions at this time.

22 March.—Quite a heavy fall of snow last night. Most of the burrow entrances were blocked, but none to a depth greater than 20 cms. In nearly all cases the adults had burrowed through this drift. It is remarkable that they should know with such precision where to dig when the whole appearance of the cliff face is changed. The marks indicate that the excavating is done with the feet.

26 March.—Further snow during the night. The wind is from the south, and with a drop in temperature the snow has been drifting over the cliff and piling up on the ledges. Most of the burrows were buried too deeply for the parents to dig their way in; one which I excavated being over 2 ft. below the surface. In the morning I watched two birds fluttering near the entrances to their nests, coming and going repeatedly, but never alighting.

2-3 April.—It began to snow about 10.00 and continued until 13.00. Then again for about 4 hours during the night. In the evening a rapid rise in temperature was accompanied by rain, and it then froze hard. A thin coating of hard ice about 3 mm. thick covered the entire moss bank. The snow beneath this thawed except in the crevices, where it remained. Every occupied burrow in the colony except 9 and 10 had been sealed up with ice—these two being sheltered from the rain and therefore only blocked with soft snow. None of the adults were able to visit their chicks.

10 April.—There has been no new snow for 3 days, but a fresh difficulty has arisen. Two days of frost and wet fog have caused a considerable growth of rime. A deposit of rough white ice growing out to windward of a small rock by burrow 15 has almost completely sealed the entrance again. The wind has been blowing parallel to the cliff face for about 24 hours, and there are marks showing where an adult attempted to scratch its way in last night.

Footprints all round the blocked burrows indicated that on most of these occasions the parents had tried to reach their chicks and failed. If the snow was soft they generally succeeded in burrowing through up to about 20 cms., but deeper drifts kept them out. Space does not permit publication of the full records, but it will be seen that the chicks frequently had to undergo periods of starvation during which they lost weight.

Owing to the long incubation and fledging periods of Wilson's Petrels, the chicks do not leave their nests until over a month later than the young of any other species which nests in Graham Land. Under the present climatic conditions, it is clear that the short summer only just permits the completion of the breeding cycle if they start nesting immediately the ground is clear of snow. There is thus evidence to suggest that the ratio of snowfall to ablation may be a critical factor in limiting the breeding distribution.¹

FEEDING

When handled, the chicks usually vomited anything up to about 2 cc. of amber-coloured oil. When they were very young this oil was clear, but as they grew older it frequently contained particles of Krill (*Euphausia superba*). I was never able to watch a chick being fed, but it is clear that the parents regurgitate partly-digested *Euphausia* for them, and that in the early stages this takes the form of a clear oil. Some of the older chicks were found to contain almost complete Krill, which could be identified without difficulty, and it is certain that when their parents can reach them they are fed at intervals, even when fully fledged. There is, in fact, no voluntary desertion by their parents as has been described for some other Petrels.

¹ The present glacial forms in Graham Land are out of accord with the existing climate and must have originated at a time when the ratio of precipitation to ablation was greater. In fairly recent times, shelf-ice filled the bays of the Graham Land coast and extended at least as far as the off-lying islands. There is not yet sufficient evidence to indicate the time at which this shelf-ice began to break out, but probably, once it began to break away, it all went out in the course of a few years. The laying bare of parts of the smaller islands such as the Argentine Islands must also have been accomplished relatively quickly once the shelf-ice had broken out. The instability of existing coastal glacier forms, and the speed of their depletion at the present day, suggest that the time which has elapsed since snow-free ground was first laid bare may be measured in terms of a few decades rather than centuries. It is thus evident that the area can only have been colonized by birds in comparatively recent times, and that further extensions of breeding range may be expected in the future. (Note based on information supplied by the Rev. W. L. S. Fleming.)

THE EFFECTS OF PERIODIC STARVATION

Fig. 11 gives the weights of some of the chicks which lost weight during known periods. The numbered nests are the same as those already discussed: A, B, and C were nests in another colony on Galindez Island. It will be noted that some of these chicks were visited by their parents, but it does not seem that they can have been fed during these visits. Of the 5 chicks which could not possibly have been fed owing to the burrows being blocked by snow, all lived except A, which died on the seventh day. The others survived after periods of starvation of 3, 5, 11 and 20 days. The last of these figures is remarkable, and it is unfortunate that the total loss of weight of this chick (No. 15) could not be measured. If, however, from the other cases we assume that it lost weight by approximately 2 grms. per day, its original weight would have been about 64 grms. Other chicks were found which weighed more than this. Chick A, which died, lost 32 per cent of its original weight during 7 days' starvation. Chick 15 would thus have sustained a corresponding loss of about 62 per cent in 20 days.

<i>Nest</i>	<i>Weight before starvation.</i>	<i>Weight after starvation.</i>	<i>No. of days.</i>	<i>Loss of weight.</i>	<i>Loss per day.</i>	<i>Notes.</i>
A.	34.0 (24.iii)*	23.0 (1.iv)	7	11.0	1.6	Burrow blocked by snow. Not visited by parents.
B.	29.5 (14.iv)	22.5 (19.iv)	5	7.0	1.4	" "
C.	? (11.iii)	? (22.iv)	11	?	?	" "
2	51.5 (8.iii)	46.5 (12.iii)	3	5.0	1.7	" ?
2	64.0 (25.iii)	56.0 (28.iii)	3	8.0	2.7	Burrow blocked by snow. Not visited by parents.
7	58.5 (28.ii)	52.0 (4.iii)	4	6.5	1.6	" ?
7	60.5 (12.iii)	56.0 (16.iii)	4	4.5	1.1	Visited every night.
8	70.5 (16.iii)	62.0 (19.iii)	3	8.5	2.8	" "
10	50.5 (8.iii)	41.5 (12.iii)	4	9.0	2.2	Visited once.
12	55.5 (4.iii)	45.5 (8.iii)	4	10.0	2.5	" "
12	64.5 (31.iii)	57.0 (3.iv)	3	7.5	2.5	" "
14	53.5 (8.iii)	45.0 (12.iii)	4	8.5	2.1	Visited twice.
15	? (9.iii)	24.5 (29.iv)	20	?	?	Burrow blocked by snow. Not visited by parents.

* Date.

FIG. 11.—Loss of Weight of Starved Chicks in grammes.

Now this figure at first seems absurdly large, but the average weight of 10 adults taken from their nests was 34.3 grms., while the heaviest chick at one time reached as much as 70.5 grms. It is therefore reasonable to suppose that eventually this chick lost about 36 grms. or as much as 51 per cent of its earlier weight. In this case, however, the loss would probably have been spread over a much longer period, for of the 4 chicks whose weight was known when they left the nest under normal conditions the average weight was 56.5 grms.

The powers of survival of Wilson Petrel chicks, when deserted by their parents, makes interesting comparison with other species. With many birds, the behaviour of the adults after the chicks have hatched is determined primarily by the necessity of shielding their young from extremes of temperature and supplying them with food at regular short intervals. Elliot Howard (1920) has shown that an absence

of no more than an hour may cause the collapse or even death of young Whitethroats (*Sylvia communis*) in their earlier stages; while Bussmann (1933) recorded with a terragraph that the young of the Great Tit (*Parus major*) are sometimes fed as often as 390 times in a day. In fact, most Passerine chicks seem to be fed more than 250 times in a day.

Of the Petrels, it has been proved in several cases that the young are fed until they become extremely fat; they then remain in the nest for a further period, unattended by their parents, and living at the expense of the accumulated fat. But little accurate information is available. Lockley (1930) found that with Manx Shearwaters (*Puffinus puffinus*) the young were entirely deserted at about the 60th day and eventually made their own way to the sea. Two nestlings were left without food for minimum periods of 11 and 13 days. Lockley (1932) considered that the same circumstances attend the fledging of the British Storm Petrel (*Hydrobates pelagicus*). Gross (1935) weighed a chick of Leach's Petrel (*Oceanodroma leucorhoa*) at intervals during the first 46 days of its life. The resulting growth curve showed considerable irregularities, which he attributed to irregular feeding. After a study of the same species, Ainslie and Atkinson (1937) gave a record of one chick which fasted for 6 days, and they suggested that finally the chicks are intentionally neglected. Their interesting table illustrating the irregularity of parental visits to 4 chicks unfortunately does not cover this final period.

Dissection of Wilson's Petrel chicks showed that the loss in weight during starvation is mainly due to the using up of the fat layer under the skin and in the body cavity. Growth of the feathers practically stops; in 7 days the longest primary of a starved chick grew 3 mm. as compared with 15 mm. in another chick of the same age which was being fed regularly. One chick was known to be about 45 days old, yet after frequent periods of starvation it had only reached the same stage of growth as another which was 15 days younger. It will thus be seen that unless a chick has reached a certain stage of growth by the time of the first winter falls of snow, it stands little chance of surviving. A similar wide variation of fledging period is known to occur in *Hydrobates pelagicus*. With this species, Lockley (1932) found the average of 6 cases to be 61 days, ranging between 54 and 68 days. He suggested that the reason for this discrepancy was due to irregular feeding.

LIMITATION BY TEMPERATURE

The young of Wilson's Petrel probably have to withstand more rigorous environmental conditions than those of any other Petrel. It therefore seemed worth while to measure the actual temperatures in a typical burrow and to consider these in relation to the temperature-regulating mechanism of the chicks themselves.

The temperatures in a typical burrow (No. 8), and of the air outside, were therefore measured with a 2-bulb thermograph. The results are shown in fig. 12. It will be seen that in spite of the marked diurnal fluctuations of the temperature of the air outside, the blanketing effect of the moss-covering evens out this fluctuation inside the burrow. During the critical time at the end of the fledging period, the chick is subjected to variations of only a few degrees, and never to a temperature lower

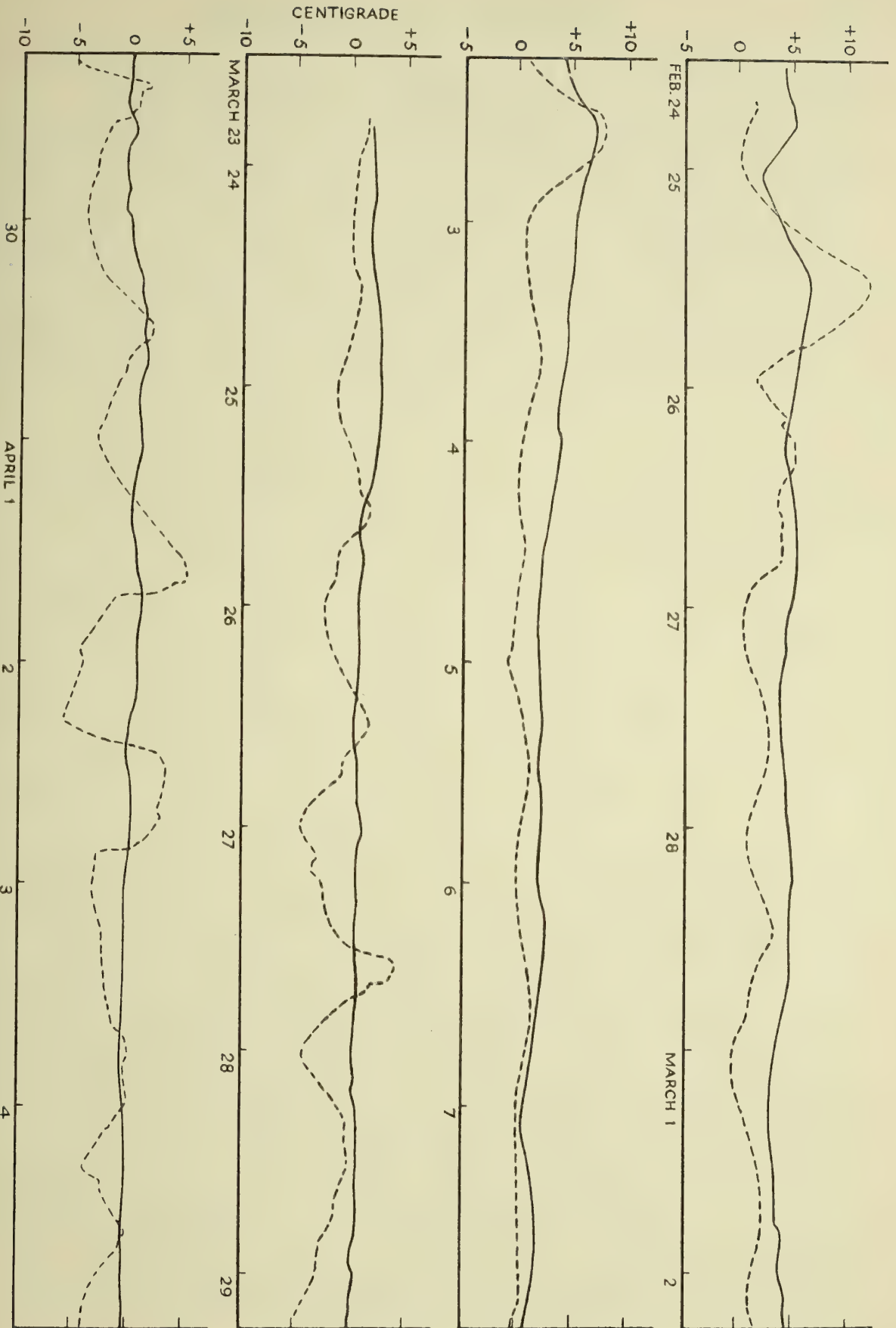


FIG. 12.—Temperature inside burrow 8 —, and of air (shade) outside - - -, during fledging period. 24 February–27 March and 23 March–4 April.

than -1.5°C . Thus the low temperature of the external environment does not affect the development of the young as much as might be supposed.

Kendeigh (1934) has shown by experiments with sparrows (*Passer domesticus*) that there is no significant difference between the survival time of starved birds in a fluctuating or constant air temperature. He found, however, that the survival time between temperatures of -10.2°C . and 33.4°C . was almost a direct linear function of the temperature, and that above the upper limit of this range the survival time began to decrease again. That is to say, there was a definite optimum temperature for living. This must also apply to Wilson's Petrel. Low temperature may not be a critical factor in itself, but it is clear from Kendeigh's work that it is a critical factor when combined with a period of time in which the chicks must remain without food.

The body temperature of a number of chicks was measured, and the results for those chicks whose age was known are tabulated in fig. 13.¹

Chick No.	Age (days).	Temperature $^{\circ}\text{C}$.
587	1	25.0
588	1	27.0
267	2	28.0
589	2	30.0
599	4	32.8
597	7	36.5
110	8*	37.0
101	10*	36.8
98	10*	36.9
99	10*	37.0
102	12*	35.2
100	18*	37.0
118	40*	37.5

* Age estimated.

FIG. 13. Body temperature of chicks.

The average body temperature of 10 adults in the breeding season was 38.8°C . (max. 40.5° , min. 36.5°). Unfortunately the time of day of these measurements was not recorded. When first hatched, the temperature of the chicks varies considerably, but after the first few days it becomes higher and more steady. The figures are not very complete, but they are sufficient to show that the chicks pass through a semi-poikilothermic stage before attaining the homoiothermic condition of the adult.

Kendeigh (*loc. cit.*) found with nestling House Wrens (*Troglodytes aë. aëdon*) that the temperature regulating mechanism does not become completely efficient until 9 days after hatching. Correlated with this is the behaviour of the adults, which brood regularly during this period, but only intermittently thereafter. The fact that Wilson's Petrel chicks are practically never brooded during the day after they are 48 hours old suggests that their temperature-regulating mechanism becomes functional after only 2 days, and this supposition is borne out by the temperatures recorded.

¹ In each case the temperatures were taken immediately after death; the thermometer being thrust down the throat and into the body cavity.

GROWTH OF DOWN AND FEATHERS: COLORATION OF SOFT PARTS

On hatching, the chick is covered with thick down which completely conceals the apteria when dry. The dorsal surface is a uniform "light seal-brown",*¹ the ventral surface usually slightly paler. The longest filaments are about 15 mm. in length. Only 6 mm. of the culmen is tipped with black; the remainder and the skin round the bill is not pigmented. A conspicuous patch of bare skin extends over the forehead, lores, chin and round the eyes, leaving a distinct crown tract, in contrast with the bald crown of newly-hatched *Hydrobates*. In a day-old chick the tarsus and toes are "pale pinkish cinnamon",* the webs "pale pinkish buff",* and the claws black. It is very feeble, and, until about a week old, supports its head by resting the tip of its bill on the ground. The eyes are kept shut until the 8th to 11th day.

The following are notes on chicks whose ages were known:

7 to 10 days.—Tarsus and toes darkening.

9 days.—Wing quills not yet sprouting.

11–12 days.—Longest wing quills 1 to 3 mm. in length, but not yet visible through the down. The tarsus and toes are "army grey",* the webs between the toes "vinaceous fawn"* becoming greyer round the edges, the bare skin on the face "pale purple drab",* and the bill "bone brown".*

15 days.—Longest wing quills are 9 mm. in length. The tips of the remiges of the juvenile plumage are unsheathed. Tarsus still darkening. With a good series of chicks I have been unable to distinguish two generations of nestling (neossoptile) down. In most of the Tubinares these are said to be quite distinct, the mesoptiles following the protoptiles by one continuous process of growth, while there is a pause between the two as indicated by the cessation of rami along the axis common to the two generations.

24 days.—Longest wing quills 19 mm. in length; primaries unsheathed and projecting 10 mm.

29 days.—Tips of retrices also unsheathed. The black juvenile (teleoptile) feathers show under the down and now cover the area on the forehead and lores which was naked at an earlier stage.

32 days.—The white juvenile tail-coverts are visible under the down which still covers the whole body. When the wings are folded the longest primaries extend 10 mm. beyond the retrices. On the primaries, secondaries and retrices the down persists only at the tips. The chick is now able to move about the burrow and is occasionally found near the entrance of the tunnel.

40 days.—Down thinning rapidly, disclosing the juvenile contour feathers. The lighter coloration of the greater wing-coverts is already distinguishable. The colour of the bill, tarsus and toes is still darkening.

45 days.—Only a few wisps of down remain on the crown, breast, mantle, back and tail-coverts.

50 days.—Most chicks have no traces of down left at this age.

The minimum fledging period recorded was 52 days, but this period may be increased indefinitely if the chick has to undergo periods of starvation. The down

¹ All colours marked with an asterisk are taken from Ridgeway's *Colour Standards and Nomenclature*. Washington, 1912.

persists longer on these starved chicks and they occasionally fly before it has all gone. The burrow is sometimes visited for several nights *after* the chick has flown, but it was not possible to determine whether these visits were made by the chicks or adults.

Fig. 14 gives measurements of some of the chicks which were preserved. Nos. 592A, 592B and 610 were found dead in their burrows in the Spring of 1937; they had evidently been blocked in by snow the previous Autumn and had died of starvation. None of these three shows traces of down, and their measurements may therefore be taken as representative of fully fledged young ready to leave the nest.

<i>Age (days).</i>	<i>Chick No.</i>	<i>Wing.</i>	<i>Tarsus.</i>	<i>Tail.</i>	<i>Toe.</i>	<i>Culmen.†</i>
1	588	12	9	0	9.5	4
2	589	13	10	0	9.5	4.5
4	599	12	11	0	9.5	5
7	595	11	15	0	10	5.5
c. 10	98	24*	22	0	19	6
c. 40	118	81*	32	22*	28	8
c. 45	117	118*	33	43*	27	8
Full fledged	592a	129*	34	51*	25	—
"	592b	101*	33	33*	28	—
"	610	127*	34	60*	28.5	7.5

* Measured to the extremity of teleoptiles.

† Measured to opening of nostril.

FIG. 14.—Chick measurements (mm.)

Apart from smaller measurements, the fully fledged chicks have the same general appearance as the adults. Murphy (1918 and 1936) states that young birds have a contour plumage differing from that of the adults in that they have conspicuous white edgings on the feathers of the belly and a whitish spot on the lores. I cannot find any constant difference between adults and young in either of these characters, but perhaps it is true to say that the concealed whitish spot on the lores is more commonly found in juveniles. Some fully fledged young have bills which are as long and wide as those of the adults, but most of them are easily distinguishable by their undeveloped nostrils.

Juvenile birds taken on 15 April, off Bahia, Brazil, were described by Murphy (1918) as having "fresh, black unworn quills and body feathers, and grey, white-edged greater coverts, at a time of the year when the feathers of old birds show the maximum effects of wear and fading." From examination of the specimens in American museums, Murphy considered that full growth is not attained until 6 or 7 months after hatching.

INFANT MORTALITY

Out of 20¹ chicks under observation at the Galindez Island colony in 1935, only 7 survived to leave the burrow. If this can be considered as normal—and all the evidence suggests that it is—the infant mortality is about 65 per cent.

In the Argentine Islands, the chief cause for this mortality was starvation due to blocking of the burrows by snow. Two chicks died owing to exposure when part of the moss bank slipped into the sea after a period of very wet weather in March. Evidence of similar landslips was found elsewhere, and such events must be counted as an occasional cause of mortality. Another chick was killed by the collapse of a rock which formed the roof of its nest cavity. Wilson's Petrels are almost the only birds in the Antarctic immune from the attacks of Skuas (*Catharacta skua*) and Giant Petrels (*Macronectes giganteus*).

FLIGHT

In spite of the fact that they can easily be distinguished apart, Wilson's and Leach's Petrel have frequently been confused at sea. Murphy (1918) has emphasized the different styles of flight of these two birds. He says: "*Oceanodroma* flies with rapid, 'leaping' strokes, quite unlike the alternations of gliding and synchronous flutters which characterize the flight of *Oceanites*." The most diagnostic point, however, and the one which Wilson himself was the first to record, is that the feet and yellow webs extend beyond the tail in Wilson's, while the short, black-webbed feet of Leach's Petrel are concealed beneath the tail.

No one who has watched Wilson's Petrel at sea can fail to be impressed by their wonderful adaptation to the environment. Often they follow a ship for hours on end, coursing back and fourth, dipping and rising with the undulations of the sea, crossing and recrossing the wake. Their flight seems almost effortless; the feet are held together, extended beyond the tail with the webs closed. The feet are dropped only when the bird stalls or approaches the water closely, and they appear to lift the bird off the surface, steadying it and helping it along. As this downward beat of the feet occurs, the webs are spread out, and the bright yellow coloration becomes visible. Wilson's Petrels do not "walk" on the water, but rather "patter" on it, lowering both feet simultaneously, three or four times in quick succession, between each short stretch of gliding. When they touch the water with their feet, they do not necessarily pick up food; they pause for a moment, with body sloping upwards at about 45°, wings fully extended, and head turned down, presumably searching the surface for food. They very rarely settle on the water, but when they do so they float buoyantly in a manner very reminiscent of *Phalaropus*. They are capable of diving, but I have only once seen a bird do this in order to obtain particles of food below the surface.

In rough weather they take advantage of the shelter afforded by the troughs

¹ This figure does not include the chicks which died owing to interference by sledge-dogs, etc.

between the waves or swell. In extra strong winds there is apparently a sharp division between the main body of the wind which passes over the crests and a series of air masses filling up the troughs and moving along with them. This view was confirmed by experiments made with smoke. Even with a strong gale blowing and a heavy swell there is a comparatively undisturbed surface of water on the windward slope of each trough. The birds follow along these windward slopes, keeping within a few inches of the surface, and taking advantage of the air currents which are deflected upwards from them. In the strongest winds I have repeatedly watched birds feeding along these windward slopes, but if they rise more than a few inches from the water they are instantly blown away downwind. Their difficulties begin when waves and swell are running in different directions. The whole surface of the sea sometimes becomes so confused that there are no definite troughs for them to fly along. On these occasions they seldom glide with rigid wings for more than a few seconds at a time, and prolonged conditions of this nature presumably may lead to exhaustion or death from starvation.

It has often been supposed that plankton organisms tend to sink from the surface layers during stormy weather, but Hardy and Gunther (1935) concluded from a vast mass of observations that the state of the sea has little or no bearing on the number of organisms in the surface layer. Even the most violent gales have little influence on vertical distribution. It would seem, therefore, that Wilson's Petrels suffer only when the surface of the sea is so confused by a combination of strong wind and cross-swell that they are unable to maintain their "pattering" over the surface in search of food.

An interesting problem is raised by the inference that Wilson's Petrel seldom, if ever, has the opportunity to sleep at any time between March and November.

MIGRATION AND DISTRIBUTION DURING SOUTHERN WINTER

We know very little about the habits and lives of Wilson's Petrels during the two-thirds of the year when they are not nesting, and almost insurmountable difficulties must be overcome before there can be any really clear picture of their oceanic migration. Reference to fig. 4 shows that they leave their antarctic breeding grounds in March or April and do not return until November or December. It is only possible to follow their movements by collecting together all the incidental observations made by the staffs of research ships and by naturalists during occasional voyages made for some entirely different purpose.

Many observers have recorded the presence of *Oceanites*, at sea, but few of them have remembered that definite information as to their absence is almost as important in working out their migration. Two authors have made notable contributions to the subject. Murphy (1918) first proved that the birds from all parts of the North and South Atlantic represent a single species, and he published observations which demonstrated beyond doubt that a migration takes place between the two areas. In a valuable summary of the ornithological literature of the North Atlantic, Wynne Edwards (1935) discusses the main characteristics of the migration in this area. I have used these two papers freely in the compilation of the following section of this

report. Other sources of information which have been used are listed in a footnote below.¹ All doubtful observations have been rejected.

THE ATLANTIC OCEAN

Twelve large maps of the Atlantic were prepared on Lambert's equal area azimuthal projection, and on each of these the positions of all the available records for one month of the year were plotted as dots, with the dates written against them. In addition, an indication was added to the appropriate map wherever a reliable observer has voyaged *without* seeing any Wilson's Petrels. The resulting distribution maps are reproduced on a very much reduced scale in figs. 15, 16 and 17. Examination of these maps immediately gives a general picture of the main movements which take place from month to month throughout the year. It must be remembered, however, that the distribution shown, especially in northern and tropical waters, is largely the result of observations from regular shipping routes. Unless this is borne in mind, the maps will suggest a concentration in certain regions for which there is no real evidence. In the same way, gaps may be due to the absence of observers, rather than of birds. The dark lines indicate the approximate limits of distribution where this could be determined from the notes of the original observers.

January.—Wilson's Petrel is confined almost exclusively to the region south of 50° S. Birds occur sparsely to 30° S., but only close to the South American coast. There are two records in tropical African waters.

February and March.—The distribution is about the same as in January, but South American records extend some 10° farther north. They appear to be absent north of about 45° S. on the eastern side of the Atlantic.

April.—As soon as breeding is done, they migrate rapidly northwards and are to be found generally distributed over the whole ocean to 30° N. The dates of first arrival at widely separated points along the eastern sea-board of South and North

¹ PUBLISHED PAPERS. (Where only a date in brackets is given, the full reference may be found on pp. 193-4.)

Allen: *Auk*, 1905; *Bull. Essex Co. Orn.*: 1926. Archer: *Birds of British Somaliland and the Gulf of Aden*, Vol. I, 1937. Ardley: (1936). Alexander: *El Hornero*, 1921. Bannerman: *Ibis*, 1912, 1914, 1920. Belcher: *Ibis*, 1914. Bent: (1922). Brewster: (1883). Chasen: *Birds of Malay Peninsula*, Vol. III, 1936. Collins: (1884). Davison: *Stray Feathers*, 1878. Dutcher: *Auk*, 1889. Eliot: *Bird Banding*, 1933. Fairbairn: *Ibis*, 1932. Falla: *Records Auckland Inst. and Mus.*, 1933, (1937). Forbes: *Ibis*, 1883. Gain: (1914). Giglioli: *Ibis*, 1881. Godman: *Ibis*, 1866. *Monograph of the Petrels*, 1907. Hanson: (1902). Von Heuglin: *Ornithologie Nordost Afrikas*, 1873. Holmes: *Ibis*, 1939. Hull: *Emu*, 1916. Hutton: *Ibis*, 1867. Jespersen: (1930). Jones and Good: *Natural History of Bermuda*, 1884. Kiyosu: (1932). Layard: *Ibis*, 1882. Lowe and Kinnear: (1930). Lucas: *Ann. Rep. U.S. Nat. Mus. for 1888-89*, 1891. Macgillivray: *Emu*, 1920. Mathews: *Aust. Avian Record*, 1917. McCormick: *Voyages of Discovery in Arctic and Antarctic Seas*, 1884. Murphy: (1936). Myers and Falla: *Condor*, 1925. Nichols: *Auk*, 1913. Nicholson and Nicholson: *British Birds*, 1931. Nicoll: *Ibis*, 1904. Paessler: *Orn. Monatsberichte*, 1911, 1915; *Journ. f. Ornithologie*, 1913, 1914. Parkin: *Ibis*, 1900. Palmer: *Proc. U.S. Nat. Mus.*, 1890. Reid: *Bull. U.S. Nat. Mus.*, 1884. Salvin: *Cat. Birds, B.M.*, Vol. XXV, 1896. Townsend: *Bull. N.E. Bird Banding Assoc.*, 1928; *Bull. Essex Co. Ornith.*, 1932. Townsend and Allen: *Proc. Boston Soc. Nat. Hist.*, 1907. Wait: *Manual of the Birds of Ceylon*, 1925. Wetmore and Swales: *Birds of Haiti and Dominican Republic*, 1931. Wilson: (1907). Wilton, Harvey Pirie and Rudmose Brown: *Rep. Scient. Results Scotia*, Vol. IV, 1908. Witherby: *Practical Handbook of British Birds*, Vol. II, 1924.

UNPUBLISHED PAPERS.

I wish to acknowledge personal communications from the following: Mr. H. G. Alexander (Voyages in the Red Sea and Arabian Sea), Mr. R. A. B. Ardley (Voyages of R.R.S. *Discovery II*, 1930-33), Mr. T. W. Bagshawe (Voyage to Graham Land, 1920-22), Dr. E. Banks (Borneo region), Mr. V. D. Carse (Voyage from South Georgia to England, 1937), Mr. F. N. Chasen (Malay Peninsula), Lieut. L. C. Hill (Voyages of *Discovery II*, 1933-38), Dr. N. Kuroda (Japan and China Sea), Mr. D. Lack (Voyage from England to Colon, 1938), Dr. R. C. Murphy (Information on specimens in the American Museum of Natural History), Mr. Neil Paton (Two voyages between England and the West Indies, 1938), Dr. A. C. Stephen (Loan of specimens in the Scottish National Museum), Dr. J. R. Strong (Voyage of *Discovery II*, 1936-37), Commander F. A. Worsley (Voyage of the *Endurance* in the Weddell Sea, 1914-16), and Prof. V. C. Wynne Edwards (Voyages in the Gulf of St. Lawrence and round Newfoundland).

I have used the original notes—now in the Library of the Scott Polar Research Institute—made by Lieut. H. L. L. Pennell and Dr. E. A. Wilson during the voyages of the *Discovery* and *Terra Nova*. In addition, I have added the data from all the relevant specimens in the British Museum, and from my own notes made during eleven different voyages in the South Atlantic.

America show that the vanguard advances with remarkable speed so that during the third week of April there is an almost simultaneous invasion of the warm waters along the entire coast of the United States. In the region off Cape San Roque, Brazil, flocks of about 200 birds are not uncommon in the middle of the month. Apparently the early migrants keep to the west side, and head for the Gulf Stream. Jespersen (1930) gives a graphic account of the passage of Petrels, most of which must have been *Oceanites*, in the Sargasso Sea. His chart, reproduced as fig. 18, gives the route of a cruise of m.s. *Dana* from St. Thomas in the West Indies, between 25 February and 2 May 1921. The days when Storm Petrels were seen are marked with black dots. He writes: "During the first part of the cruise, viz. from 25 February to 31 March, Storm Petrels were observed on 3 days only and then only a single bird at a time. During the following 8 days, viz. from 1 to 8 April, Storm Petrels were seen on 2 days, from the 9th to the 16th on 5 days, from the 17th to the 24th on 5 days, and from 25 April to 2 May on 8 days. The number of birds seen also increased steadily during the last 2 or 3 weeks of the cruise. There can thus be hardly any doubt that the great increase in the number of Storm Petrels during April is due to an influx of these birds from some other place, and though Capt. Hansen was unable to distinguish the species of these birds, everything points to their having been especially *Oceanites oceanicus* which in the Spring were on their way, migrating from the southern hemisphere."

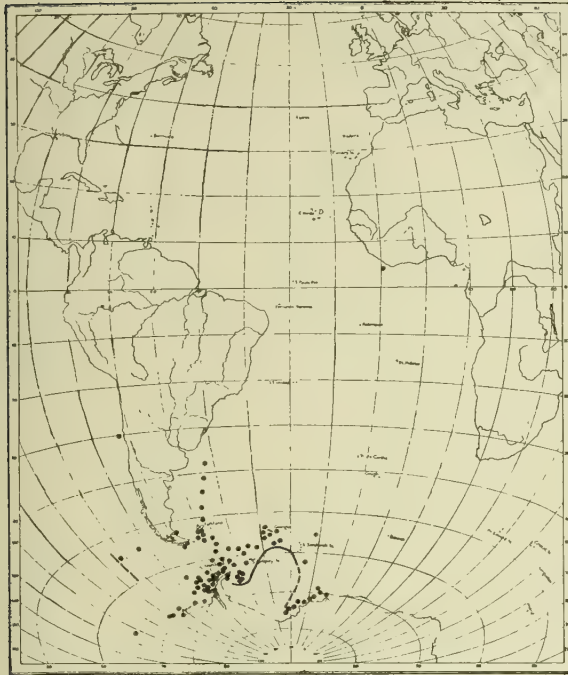
All the evidence suggests that the main migration passes between St. Paul's Rocks and the Brazilian coast. Considerably fewer birds pass up the African coast, and here the vanguard lags behind so that by the time they are already numerous in 40° N. on the west side, the foremost birds have only reached 10° N. on the east side, while in the Central Atlantic they are still south of the Equator.

May.—Migration continues through tropical and American waters. An interesting point is the definite absence of records in the central parts of both the North and South Atlantic. During May, Wilson's Petrels have only been observed four times in the eastern North Atlantic,¹ and to the west they have begun to work inshore towards the United States. In the southern hemisphere there is only one record south of 40° S. A few are present off South Africa.

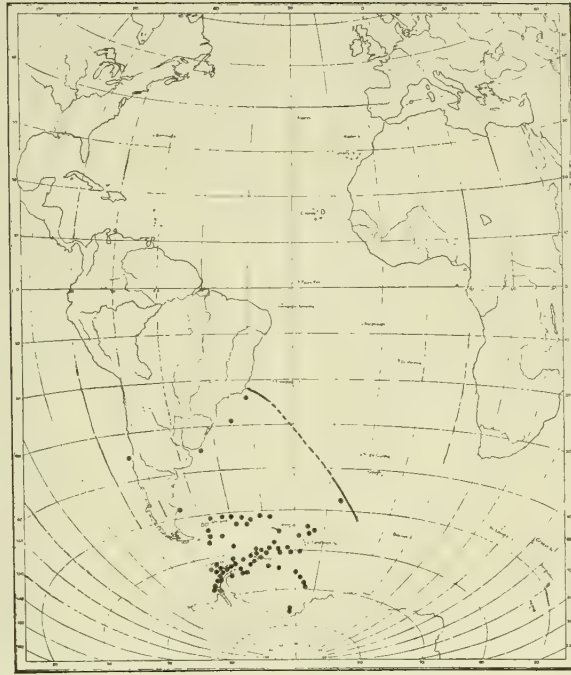
June.—Completely absent south of the Equator in the Atlantic, but distributed between 5° and 40° S. on the west coast of South America. In the North Atlantic they continue to work inshore on both sides, and are absent from the great expanse of ocean between 20° and 65° W. They literally "swarm" along the United States coast at this time. On 30 June 1913, J. T. Nichols (Bent, 1922) estimated that from a point on the crest of the dunes at Mastic, Long Island, at least a thousand Wilson's Petrels were within binocular range at one time. Similar observations have been made by other observers during July and August.

July and August.—These two months may be combined in an attempt to outline the distribution in the height of summer. Wynne Edwards (1935) has already given an able summary of the main facts. The only records for the central North Atlantic come from Townsend (1928) who saw them daily from a point not far south-west of Ireland all the way to Boston in July 1927, and from Neil Paton who informs me

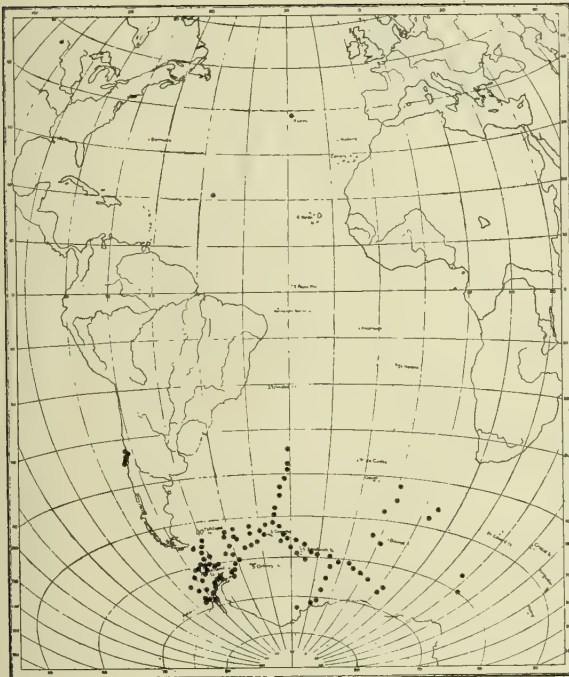
¹ Gould claims to have seen large numbers off Land's End, England, in May 1838, a highly abnormal circumstance which has never occurred in the intervening century.



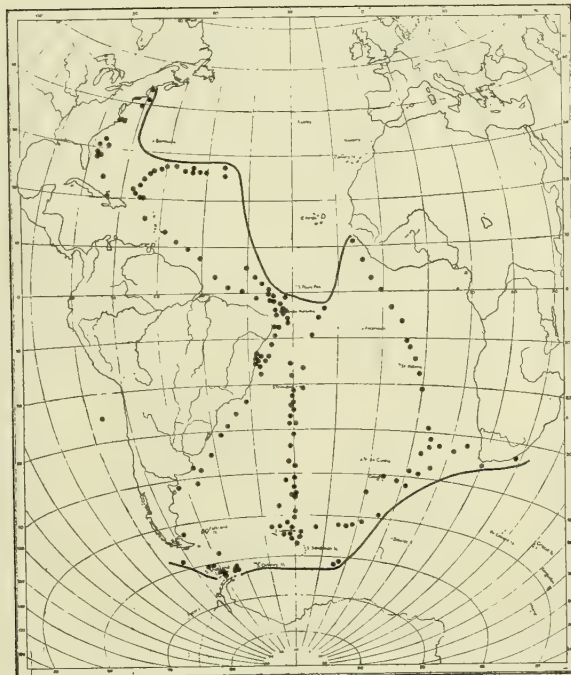
January.



February.



March.



April.

FIG. 15.

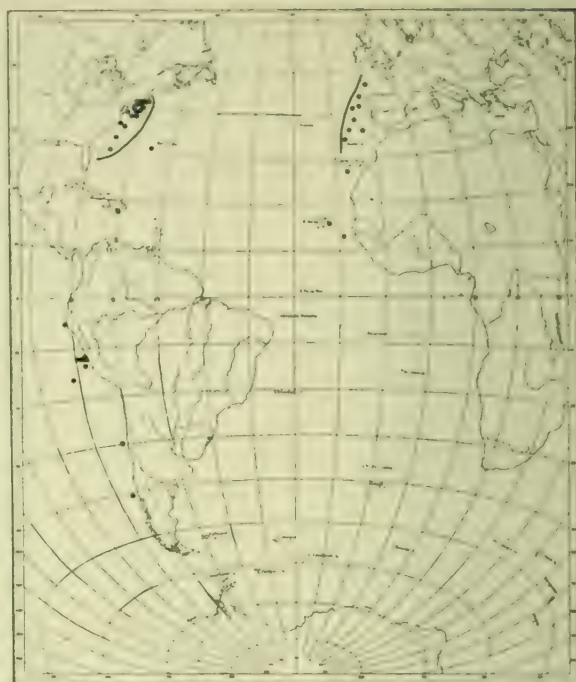
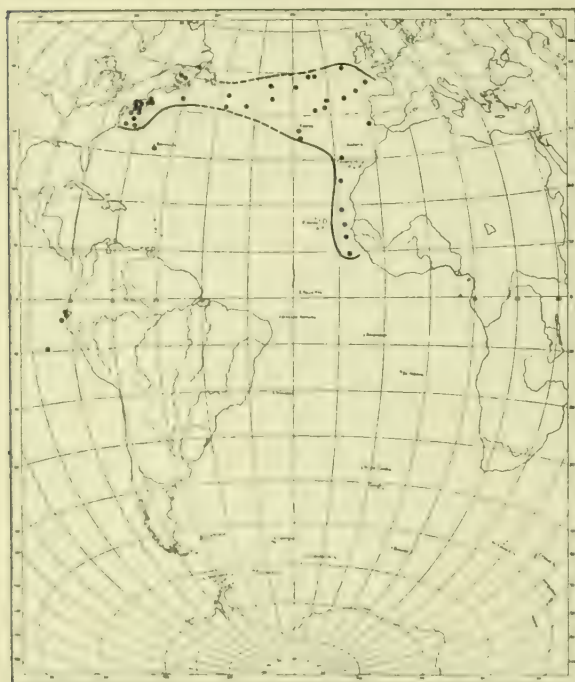
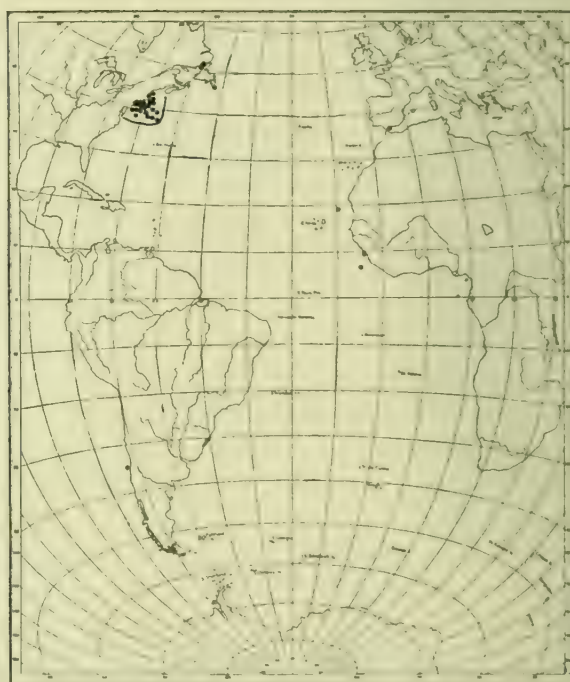
*May.**June.**July.**August.*

FIG. 16.

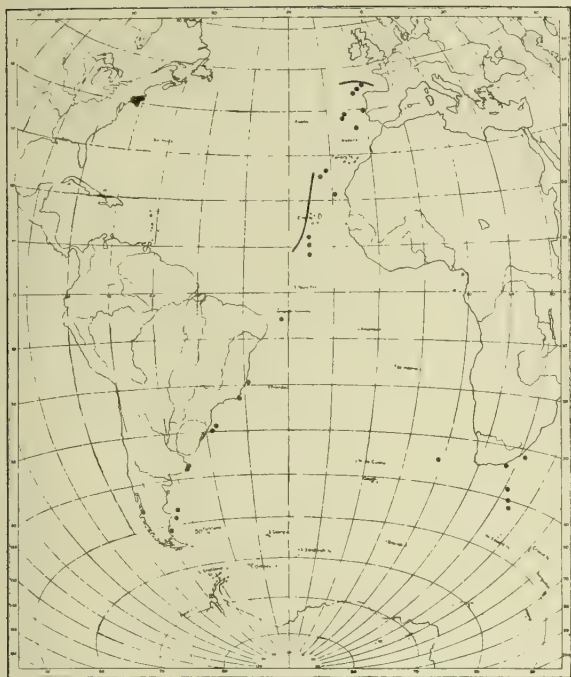
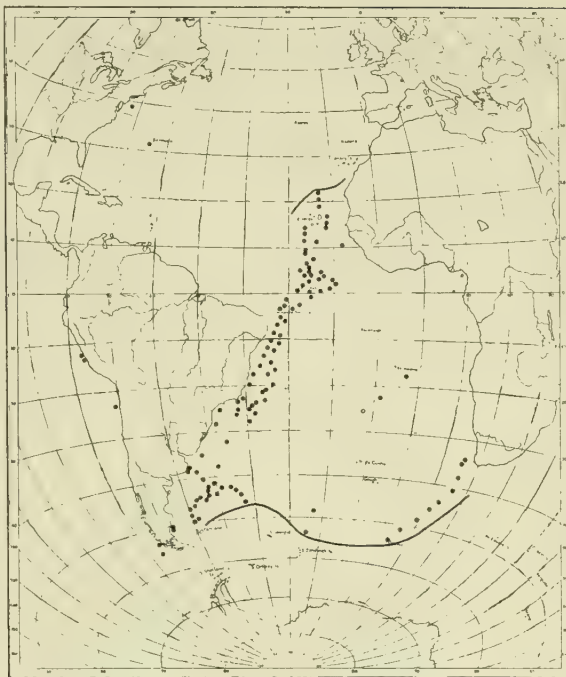
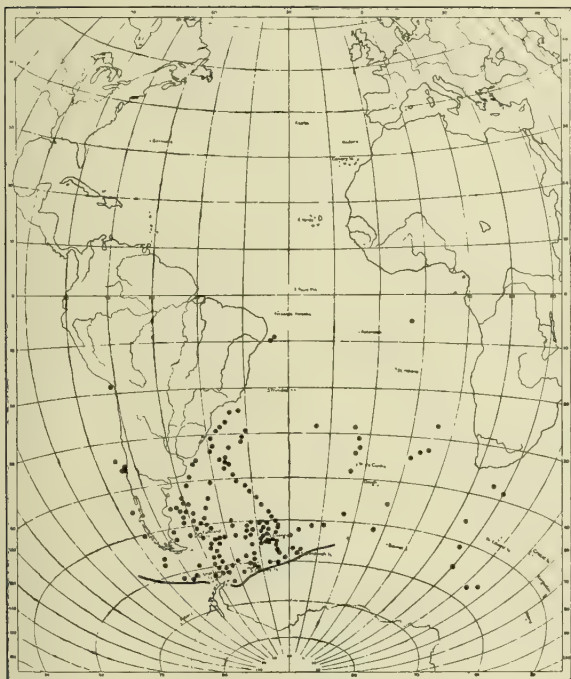
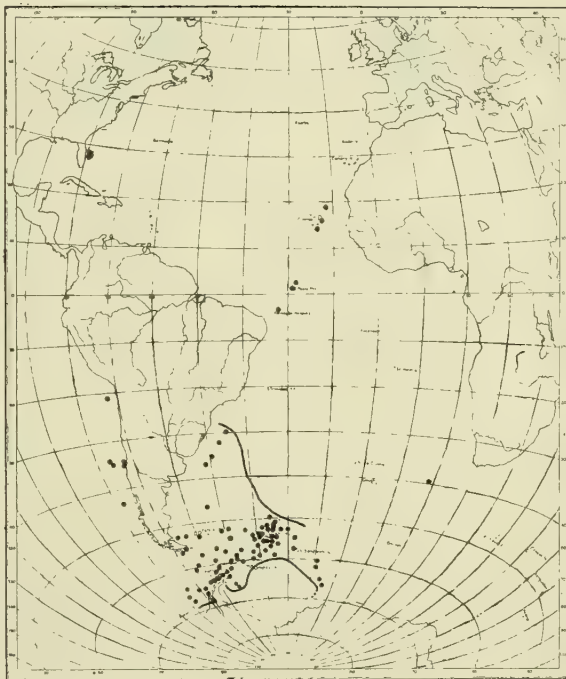
*September.**October.**November.**December.*

FIG. 17.



FIG. 18.—Observations from *m/s Dana* in the Sargasso Sea from 25 February to 2 May 1921. The route from 25 February to 1 April is marked with a dotted line, and from 1 April to 2 May with a continuous line. The black dots indicate where Storm Petrels were observed. After Jespersen (1930).

(*in litt.*) that he found them in large numbers between 40° N., 48° W., and 50° N., 15° W. at the end of July 1938. Apart from these records, they appear to be absent from the region between 30° and 60° W., and are evidently most numerous in the Gulf Stream off the American coast.

As regards the extreme northern limit reached, there does not seem to be any reliable evidence of their presence north of lat. 52° 30' in American waters. Statements that Wilson's Petrel ranges north to Davis Strait appear to be founded on erroneous identification. Wynne Edwards (*loc. cit.*) summarizes the most northerly records on the American side. He has since made several summer voyages in Newfoundland waters and has kindly sent me some additional notes from this area. Off Nova Scotia and southwards they occur annually in great numbers. In July and August there are nearly always a few in the Gulf of St. Lawrence, and probably more on the Grand Bank, but evidently the numbers vary considerably from year to year. The most northerly authentic record appears to be a specimen from Bonne Espérance, west of the Straits of Belle Isle (51° 25' N., 57° 42' W.), and now in the National Museum of Canada. Townsend and Allen (1907) picked up a pair of wings in August 1906, at Battle Island, about 30 miles north-west of Belle Isle. On the other side of the Atlantic, Wilson's Petrel extends its northward range to the Bay of Biscay. Stragglers have occurred off the coast of Provence, but in the British Isles it is a very rare vagrant. Witherby (1924) gives several authentic records, the northernmost of which is from Jura in the Outer Hebrides. There are several specimens from the Mediterranean in Museums, but most of the labels do not give exact localities. One was obtained off Malaga (Godman, 1907), and another off Sardinia (Giglioli, 1881).

September.—The return migration has begun. Some birds linger off Long Island and off the Spanish coast throughout the month, but the majority have already left northern waters and are to be found scattered as far south as the Falkland Islands and South Africa.

October.—Migration is in full swing, and there are sufficient records to define the southern limit with some confidence. The observations for September and October suggest the possibility of a movement from west to east in the North Atlantic at this time; certainly the American coast is evacuated before Africo-European waters. Again the main passage route in the southern hemisphere appears to follow the South American coast. The large number of records from the shipping routes on the west side, and their complete absence from those on the east, is too striking to interpret in any other way.

November.—The foremost birds have already reached their breeding grounds in West Antarctica, and the southern limit of their distribution is co-incident with the northern limit of pack-ice. There are no reliable records north of the Equator.

December.—Apart from three exceptional records in the neighbourhood of the Cape Verde Islands, and one near St. Paul's Rocks, none have been seen north of 30° S. The observations for this month again demonstrate the concentration in the western part of the South Atlantic.

It will be noted that, even in the midst of the breeding season, non-breeding birds are dispersed over the southern ocean. Furthermore, an occasional Wilson's Petrel may be seen in tropical waters throughout the whole year. It is almost certain (see p. 160) that the juvenile birds do not breed until 2 years old, and that the whole of

this period must be spent at sea. Herein lies a probable explanation of the occurrence of *Oceanites* in the tropical Atlantic during the southern summer. Where the majority of them spend their first northern summer is not yet known. If we may judge from collections, they constitute only a very small proportion of the birds occurring along the coast of the eastern United States, but they are common in tropical South American waters. Possibly they make a less extensive migration than the adults. It is certain that there is a definite north and south migration of these non-breeding birds.

THE PACIFIC AND INDIAN OCEANS

Scarcity of observations makes it hard to elucidate the migration in the Pacific and Indian Oceans. All the available records were plotted on monthly maps in the same way as for the Atlantic, but so few reliable ornithologists have voyaged in these seas that the information on these maps is too fragmentary to warrant their full publication. However, they do give a general picture of the movements, and have made possible the following summary:

December, January, and February.—The great bulk of the existing records are from the extreme south in the three months when exploring ships have steamed through the pack-ice and visited the Antarctic coastline. Fig. 19 shows the distribution of all the December, January, and February oceanic records which I can trace.¹ It will be seen that there are none anywhere north of 50° S. during these months. The actual position of the northern limit at this time has only been noted on nine occasions, when ships travelling in a north or south direction have passed out of or into the region where the birds occur. These nine positions are given with their dates. The arrows show the direction in which the observers were going.

The birds are concentrated mainly in the vicinity of their breeding grounds, but are also found generally distributed up to about 800 miles from land.

March.—The northward migration has begun. There are scattered records between 30° S. and 60° S. Some birds still linger off the Antarctic Continent.

April.—There is evidence to suggest that in the Indian Ocean there are none present north of about 30° S., and the known records are all off South Africa between 40° and 65° E. In the Pacific we have only three April records: one on the 15th off Guadalcanar Island, and another on the 30th off Bougainville Island—both in the Solomon Islands (Whitney South Sea Expedition). The third is from Japan (Kiyosu, 1932). Dr. N. Kuroda has kindly sent me a translation of the account of the capture of this bird which took place at the Inubôgasaki Lighthouse, Hondo (35° 39' N., 140° 53' E.) on 6 April, 1929. He also examined the skin for me and there can be no doubt as to the authenticity of this unique record. Dr. Kuroda tells me that he can trace no other references to *Oceanites* in the China Sea region.

May.—Migration is evidently in full swing; the birds appear to be well scattered, but observations from *Discovery II* show that they are absent south of 40° S., east of 90° E. Hutton (1867) found them common on 2 May in lat. 39° S., long. 33° E., and later saw occasional birds as far east as long. 88° E. in the same latitude. MacGillivray (1920) saw one on the 25th "a day's steam W.N.W. of Freemantle", and

¹ With the exception of one which is apparently quite abnormal. On 2 December 1925, the Whitney South Sea Expedition captured a female in lat. 38° S., 179 W., east of North Island, New Zealand.

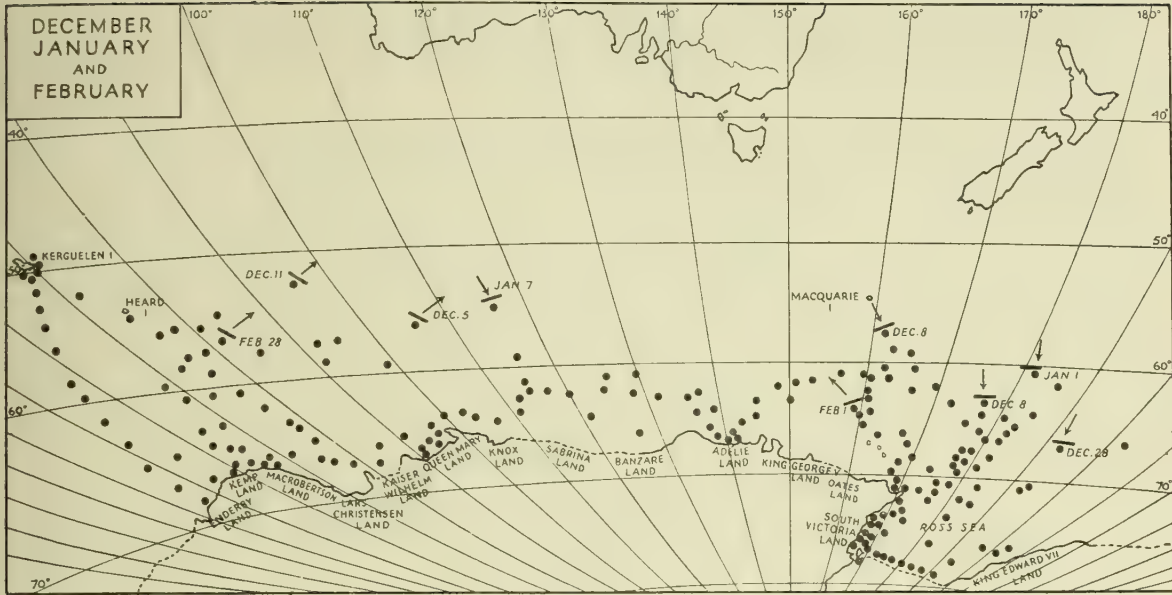


FIG. 19.

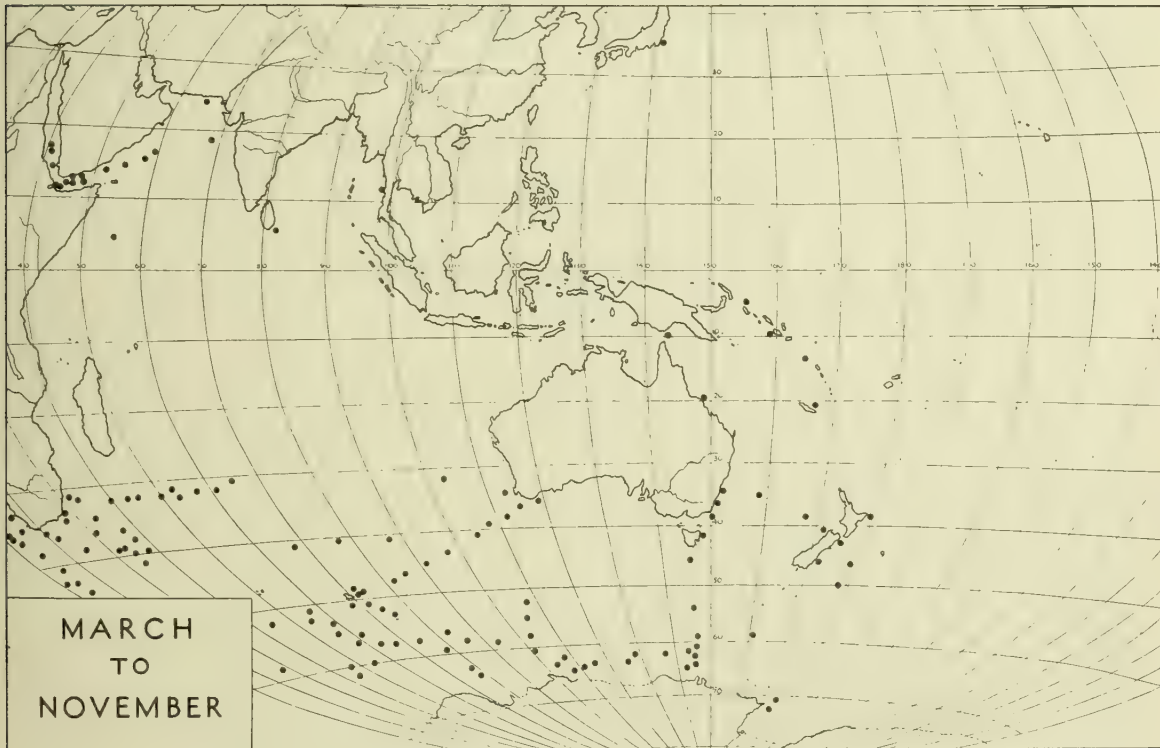


FIG. 20.

(Aitoff's Equal Area Projection).

there is a specimen in the British Museum taken on the 28th in the Arabian Sea off the Mekran coast. In the Pacific I can only trace three records: one from Gisborne, New Zealand on the 31st (Falla, 1933); another from Port Bowen, Queensland, on the 27th (Mathews, 1917); and several off the south coast of New Guinea on the 13th (Nicoll, 1904).

June, July, August, and September.—Absent from the Southern Ocean. In the Pacific one was shot on 21 June off the east coast of New Caledonia (Layard, 1882), and another in the Solomon Islands on 27 July (Whitney South Sea Expedition). Davison (1878) saw large numbers towards the end of July one year off the Tenasserim coast, Malay Peninsula, and there is some evidence that *Oceanites* has occurred in the Straits of Malacca (Chasen, 1936). All other records for these 4 months are from the Arabian Sea and the Red Sea. In the American Museum of Natural History there is a specimen from the Seychelles taken on 18 June. Mr. H. G. Alexander has kindly sent me some interesting unpublished notes made during his voyages across the Arabian Sea. In 1927 he left Aden on 11 September and reached Bombay early on the 16th. Wilson's Petrels were plentiful in the southern part of the Red Sea on the 10th; they were common on the 11th and 12th; none were seen on the 14th, but one was seen on the 15th. Returning in October, he saw a few on the 21st in lat. 14° N. long. 52° E. In 1930 he saw several in the Red Sea in lat. 16° N., long. 41° E. on 2 August, and others off the Arabian Coast during the two following days. Additional evidence comes from Archer (1937), who saw Wilson's Petrels on several occasions while crossing from Berbera to Aden. Northward-bound from Aden on 5 September 1929, he describes how they were "scattered over the sea in every direction as far as the eye, aided by binoculars, could reach; and there was no abatement in their numbers till the Straits of Bab-el-Mandeb were left behind after a run of 100 miles. Certainly *many, many thousands* were seen, and they were clearly on passage." As long ago as 1873, von Heuglin recorded the presence of Storm Petrels in September and October about Bab-el-Mandeb and the Gulf of Tajura. He was unable to secure specimens, but thought they were *Procellaria pelagica*. It now seems certain that these birds must have been *Oceanites*.

In view of these records, it is clear that Wilson's Petrel visits the west side of the Arabian Sea and the southern part of the Red Sea in considerable numbers from late July or August until late October. There is apparently a concentration in this region analogous to the Atlantic concentration off the eastern sea-board of the United States. However, if this is a regular occurrence, it is difficult to understand why it has not been recorded more frequently in a region which must have been crossed by so many ornithologists.

October and November.—Southward migration has begun. The records mentioned above show that some birds still linger in the Arabian Sea in October, but they are also well scattered southwards. There is a specimen in the British Museum from lat. 32° S., long. 52° E., taken on 19 October. One was captured off Ceylon as late as November (Wait, 1925). Farther east, in the Pacific, the Whitney South Sea Expedition captured one near the Napanui Group, Swallow Islands, on 14 October, and three off Torres Island, New Hebrides, on 23 October. Hull (1916) records two off the coast of New South Wales in October 1913, and Belcher (1914) noted occasional birds during a voyage from Sydney to Dunedin between 24 and 29 October.

In November there are no records north of latitude 40° S., and the main body of the migration has already passed 50° S.

All the available information from March to November has been summarized in fig. 20. It would seem that the main northerly goal of the migration across the Indian Ocean is in the extreme north-west, and this is confirmed by the absence of records from the northern part of the Bay of Bengal and the Malay Archipelago. The few specimens from the New Hebrides-Samoan area have a special interest in suggesting that there is a migration across this region. It seems possible that some birds may spend part of the southern winter in the open ocean to the north of New Guinea.

In the eastern Pacific, a separate stream of Wilson's Petrels migrates northwards up the Peru Coastal Current. Records from the west coast of South America have been plotted on figs. 15, 16, and 17. There are observations and specimens from many localities as far north as Callao, Ancón and the Guna Islands. A single specimen was taken off Monterey, California, in August 1910 (Bent, 1922), but no others have been seen north of 8° S.

To summarize: The migration of Wilson's Petrel is one of the longest and perhaps the most remarkable of any bird known. From their antarctic breeding grounds they fly northwards every year, extending to Newfoundland and the British Isles in the Atlantic, to the Red Sea and Persian Gulf in the Indian Ocean, to New Guinea and northern Peru in the Pacific. In a straight line the Atlantic migration is about 7000 miles in each direction, yet the flight throughout is indirect and quite unlike that of land birds crossing the sea. For the greater part of 8 months most of them probably never come within sight of a landmark, yet they return at almost the same date each year to the same burrow and mate. Oceanic migration of this type provides a noteworthy example of powers of endurance, and it also raises the problem of orientation in its most difficult form. In view of such facts it is extraordinary that visual memory is still quoted as the most satisfactory explanation of the way in which birds orient themselves during migration.

Owing to the close similarity of birds from the different breeding localities, it is seldom possible to determine the origin of birds captured during migration (see p. 154).

MOULT

For a discussion of this subject the reader is referred to Murphy (1918, pp. 117-122). After plotting on a map the dates and positions of moulting adult specimens from various museums, I am led to the conclusion that a complete moult takes place during migration between May and October. Peruvian specimens taken by R. H. Beck in May and June were practically all undergoing moult of the wing quills. Birds in similar condition have been taken in June at such widely separated localities as Cape Finisterre, French Equatorial Africa and the Atlantic coast of the United States. Moulting specimens have also been taken at various points along the west coast of Africa between June and September. Specimens taken between July and September off Long Island and the coast of New England show that the loss and replacement of the flight feathers is finished by about the end of August, but that the renewal of the body plumage is slow and irregular and may not be completed before the end of September. I can confirm Murphy's opinion that the remiges are lost before

the retrices and that the primaries are lost in succession from the inner towards the outermost feathers, which are the last to go. Murphy also states that "the moult of the retrices is, in general, from the central towards the outer feathers, nearly or quite symmetrically, the coverts moulting at the same time."

Birds have been taken in full moult off Magallanes (March), Callao (October), Aden (November), and Massachusetts (January). Probably some of these are juveniles which apparently undergo no moult until after they have left the coast of the United States in August or September. Many more specimens must be collected before the plumage changes can be adequately worked out.

Before the moult, the whole plumage is of a lighter colour than it is afterwards. Contrasting with the new "fuscous black"* feathers which replace them, the old faded ones vary in colour between "buffy brown"* and "olive brown"*. The pale tips of the greater wing coverts become less conspicuous as the feathers fade. This pale edging is an extremely variable character and does not appear to be of any value in distinguishing the different races (see Falla, 1937, p. 208). It occurs, to a greater or less extent, in specimens which I have examined from nearly all the breeding localities. Microscopic examination shows that in birds with worn plumage the white tips become abraded away from the greater coverts. The old feather tips are characterized by the absence of barbicels, missing or withered barbules, and bleaching of the pigment granules. Such feathers afford a good demonstration of the way in which pigment helps to resist abrasion, for the white parts suffer most.

ADULT MORTALITY

There is little accurate information on adult mortality. In the Antarctic, only one case is known to me in which they have formed the prey of larger birds. At Cape Adare, Priestley (1914) shot a McCormick's Skua (*Catharacta skua maccormicki*) which had a half-digested Wilson's Petrel in its stomach. It is probable that they are sometimes captured by surface-feeding fishes. One taken from a nest on Galindez Island had a foot missing, and birds with only one leg have several times been noted in the North Atlantic.

Exceptionally bad weather sometimes proves too much for them during migration. Pearson (1899) describes the results of a great storm which raged on the coast of North Carolina on 28, 29 and 30 August 1893. Thousands of Wilson's Petrels were washed ashore so that the 10 miles of beach from Beaufort Harbour to Cape Lookout was literally strewn with them: "many were dead; others were alive but too weak to fly. In places two or three would be lying together; at certain points for a distance of many feet the ground would be completely covered with bodies, sometimes piled two or three deep. . . . In the cove the slaughter had been tremendous. Thousands of birds sat or lay on the ground, covering the beach like a blanket, extending from the water's edge up into the grass on the higher ground. The fishermen of the neighbourhood carried home with them baskets filled with these birds to eat."

CALLS

Except during the breeding season, Wilson's Petrel is normally a silent bird. I have already mentioned the harsh chattering call which is repeated in the burrow

during courtship (see p. 161). When pairs are calling to each other—one being outside and the other inside the burrow—and also when they are captured, they utter a rapid succession of short high-pitched “peeps”. In addition, they have another call, not unlike the querulous chattering of a sparrow (*Passer domesticus*), which is most commonly heard when they are feeding at sea. This call is repeated more rapidly when they become excited at the abundance of food, but I have occasionally heard it in the breeding colonies.

FOOD

The majority of stomachs examined were found to contain an amber-coloured oil. In the Graham Land region the only food identified was Krill (*Euphasia superba*), and it is probable that throughout the antarctic breeding areas, their normal diet is composed of these Crustaceans. Among the birds observed and collected by Falla (1937) in Royal Sound, Kerguelen, the main food was an abundant amphipod (*Euthemisto* sp.), but he found *Euphasia* in the stomachs of specimens which he captured along the antarctic coastline. Two from Cape Denison contained “small Cephalopod remains”.

Like other Petrels, *Oceanites* has a strong sense of smell. Oil or fat of any sort, spread upon the water, will quickly attract them if they are in the neighbourhood. Many authors have noted great numbers congregated round dead whales, and the southern whaling industry must have led to a complete change of feeding habits in some areas. From February to May huge flocks come into the South Georgia whaling stations to feed on the floating oil globules and fat particles, but even the immense numbers in South Georgia do not seem to approach those which used to collect in the sheltered harbour of Deception Island, in the South Shetlands, when a whaling station flourished there between 1914 and 1931. Some idea of the concentration which used to occur at this feeding place close to the breeding grounds is given in a photograph taken in 1925 by Mr. A. G. Bennett to whom I am indebted for permission to publish it here (plate VI). Wilson's Petrels also collect round the pelagic whaling factories. Falla (*loc. cit.*) writes that in February 1931 there were as many as 5000 or 6000 attending the factory ship *New Sevilla* (67° 10' S., 74° 28' E.), and feeding on oil sum. Such large numbers as this appear to be exceptional; I have been informed by whalers that 300 to 400 is more usual in the open sea.

When the birds migrate northwards in the southern winter, their feeding habits are again affected by man. Presumably they still take Crustaceans, but they seem to prefer the oily substances connected with the fishing industry. All along the east coast of North America, wherever a boat stops to fish, the scattered Petrels are at once attracted by the refuse which is thrown overboard. Fish “gurry” of all sorts is taken, and it is rather remarkable that nothing else has yet been certainly identified from the stomachs of birds taken in the North Atlantic except a few otoliths of small fishes and an assortment of crystalline lenses, apparently from small fishes, in three specimens collected off the Cape Verde Islands (Murphy, 1918).

They are so tame that it is quite easy to watch them at close quarters as they feed on globules of oil or fat on the surface of the water. While feeding, they flutter their wings and tread water; their legs are partially immersed, but the feathers do

not get wet. They remain hovering for 3 or 4 seconds in this position, and it is possible to see the oil globules decrease in size and disappear as they are sucked up. Usually they deal with food in small particles, but they have been watched feeding on large chunks of refuse, "standing" on the water, with quivering wings held high as they pull at the food.

PARASITES

In Graham Land a number of Wilson's Petrels were examined for external parasites. Most of these carried Mallophaga which all proved to belong to a single species not previously described. The Mallophaga collected during the Expedition will form the subject of a separate report. I am indebted to Miss T. Clay for the following note on the specimens from *Oceanites oceanicus exasperatus*, which, prior to a revision of the genera from Petrels, she has temporarily placed in the genus *Naubates*.

"This species is most nearly related to a new species found on *Garrodia nereis* and to *Naubates annuliventris* Uchida, found on *Oceanodroma furcata*. These species are of considerable interest as they appear to form a link between the *Synautes*—*Halipeurus* species on one hand and the *Naubates* species on the other.

"There are no other species described from *Oceanites oceanicus*, but *Synautes languidus* Kellogg and Kuwana has been described from *Oceanites gracilis galapagoensis* (Lowe)."

The complete gut from 6 adult Wilson's Petrels was washed out with 1 per cent saline solution, but careful examination disclosed no intestinal parasites.

UTILIZATION BY MAN

I have been only able to trace two insignificant but none the less interesting cases in which Wilson's Petrels have been put to practical use by man. In South Georgia, a man who had been sealing on Kerguelen Island 40 years ago told me that their habit of ejecting oil had led the old sealers to make them serve the purposes of a candle by drawing a wick through the mouth and anus. Until quite recently there was a similar custom in south-west Ireland where the inhabitants of the Blasket Islands used candles made from a rush drawn through the oily body of a Storm Petrel (*Hydrobates pelagicus*).

Collins (1884) records that Wilson's Petrels were formerly used as bait by the New England cod-fishermen when other sources of bait were lacking. His description of the method which was used for catching them bears witness to the great numbers present on the fishing grounds:

"The most common and effective way of killing them was with a whip, which was made by tying several parts of cod-line—each part 6 or 8 ft. long—to a staff 5 or 6 ft. in length. The Petrels were tolled up by throwing out a large piece of codfish liver, and when they had gathered in a dense mass, huddling over the object which attracted them, swish went the thongs of the whip, cutting their way through the crowded flock and perhaps killing or maiming a score or more at a single sweep. By the time these were picked up another flock was gathered, and the cruel work went

on until, maybe, 400 or 500 birds were killed, though perhaps it was seldom that so great a number was obtained at once."

However, the superstition among sailors that it is unlucky to kill a "Mother Cary's Chicken" has largely protected them.

SUMMARY

The life-cycle of Wilson's Petrel (*Oceanites oceanicus*) is discussed as a result of studies made in the Antarctic during the British Graham Land Expedition, 1934-37. Records and observations of other writers are incorporated to provide a summary of all that is known of the species.

In an introductory section, the history of Wilson's Petrel is briefly reviewed from the time of its discovery in 1813, and the known breeding localities are listed. Measurements of 113 specimens from these localities are tabulated and discussed with the aid of statistical methods. Four population groups are given subspecific status:

Oceanites oceanicus oceanicus (Kuhl).

South Georgia.

Oceanites oceanicus exasperatus Mathews.

Graham Land, South Shetlands, Queen Mary Land, Adélie Land, and South Victoria Land.

Oceanites oceanicus parvus Falla.

Kerguelen Islands.

Oceanites oceanicus magellanicus nom. nov.

Falkland Islands and Tierra del Fuego.

The four populations differ only in the mean of their measurements, the birds becoming progressively larger as higher latitudes are reached. There is no variation in plumage which lies outside the known range of variation from any one locality. Reference should be made to p. 154, where the identity of migrating birds is discussed.

Breeding habits were studied at a colony in the Argentine Islands in West Graham Land. Twenty-three burrows were excavated and the birds kept under daily observation throughout the breeding season. Courtship is mutual, taking place partly during evening flights round the colony and partly inside the burrow. The visits of the adults to a burrow during this period were automatically recorded with a thermograph.

Incubation is shared equally by both sexes which take alternate spells of approximately 48 hours. The incubation period of 9 eggs ranged from 39 to 48 days. The average measurements of 20 eggs are given.

The fledging period is subject to considerable variation owing to irregular feeding by the parents. Growth curves of 6 chicks show that there is an initial period of steady gain in weight, lasting about 2 weeks, followed by a protracted period of fluctuations. Losses in weight are correlated with snowfall which frequently blocks the burrow entrances and prevents the parents reaching their chicks. The effects of the resulting periods of starvation of the chicks are discussed and compared with similar observations on other species. The chicks are fed at night whenever their

parents can reach them, and they are not voluntarily deserted by their parents when fully fledged as has been described for some other Petrels. They attain more than twice the weight of the adults, and are able to survive as much as 20 days without food. The minimum fledging period recorded was 52 days, but this may be considerably prolonged since growth practically stops while the chicks are not being fed. In Graham Land their diet is exclusively Krill (*Euphasia superba*).

The chicks pass through a semi-poikilothermic stage before attaining the homoiothermic condition of the adult. Thermograph records of the temperatures in a typical burrow are given. The growth of the down and feathers and the coloration of the soft parts at different ages are described. In the Argentine Islands, chick mortality was about 65 per cent. The causes of death are discussed.

The annual migration from the Antarctic to the northern hemisphere is discussed and illustrated by monthly distribution maps. The migration is one of the longest and perhaps the most remarkable of any bird known, extending to Newfoundland and the British Isles in the Atlantic, to the Red Sea and Persian Gulf in the Indian Ocean, to New Guinea and Northern Peru in the Pacific. Ringing results prove that they return each year to the same mate and burrow in the Antarctic. Juvenile birds probably do not breed until at least their second year.

A complete moult takes place during migration between May and October.

Other sections of the paper deal with flight, adult mortality, parasites, call-notes, and utilization by man.

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FIG. 1



FIG. 2

The moss patch in the Argentine Islands where most of the observations were made. The colony was along the cliff-edge in the centre of the picture.

FIG. 1.—as it appeared in November, when the birds first arrived; and FIG. 2.—in January when most of the snow had melted away.



FIG. 1.—Adult Wilson's Petrel incubating (burrow excavated).

*Photo A.A.E., 1911-14, by permission of
Sir Douglas Mawson.*



FIG. 2.—Adult entering burrow (flashlight).



FIG. 1.—Chick 10 days old.



FIG. 2.—Excavated burrow to show "lid" above nest cavity and numbered peg.



Photograph by Howard Cleaves

Migrants feeding in Lower New York Bay, U.S.A.



Photograph by Howard Cleaves

Adult in typical attitude while feeding.



Photograph by A. G. Bennett

Wilson's Petrels feeding on oil refuse, Deception Island, 1925.



X-ray photograph of adult Wilson's Petrel. Note the great length of the legs.

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BRITISH GRAHAM LAND EXPEDITION

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THE BREEDING BEHAVIOUR OF PENGUINS

*WITH SPECIAL REFERENCE TO
PYGOSCELIS PAPUA (FORSTER)*

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WITH FOUR PLATES AND TWENTY-SIX TEXT FIGURES

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Malgré la diversité apparente des amusements qui semble m'attirer, ma vie n'a qu'un objet. Elle est tendue tout entière vers l'accomplissement d'un grand dessein. J'écris l'histoire des Pingouins. J'y travaille assidument, sans me laisser rebuter par des difficultés fréquentes et qui, parfois, semblent insurmontables... Il est extrêmement difficile d'écrire l'histoire. On ne sait jamais au juste les choses ne sont passées; et l'embarras de l'historien s'accroît avec l'abondance des documents. Quand un fait n'est connu que par un seul témoignage, on l'admet sans beaucoup d'hésitation. Les perplexités commencent lorsque les événements sont rapportés par deux ou plusieurs témoins; car leurs témoignages sont toujours contradictoires et toujours inconciliables.

ANATOLE FRANCE, 1907

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INTRODUCTION

THIS paper forms the first of a series of studies of Penguins (*Sphenisciformes*) resulting from data gathered during the British Graham Land Expedition, 1934–37. The observations were carried out in numerous localities in West Graham Land, the Falkland Islands, and South Georgia. The main object of the Expedition was geographical, and the biological programme was necessarily dependent on unavoidable changes in plan which frequently made it impossible to carry out extended observations in any single locality. Nevertheless, there were opportunities to visit a very large number of penguin colonies of seven different species, and to see a wide variety of stages in their life cycles. The specimens collected, and the details of life histories, distribution, numbers, etc., will be discussed elsewhere.

The present paper deals chiefly with the behaviour phases of the breeding season. In particular it is concerned with the Gentoo Penguin (*Pygoscelis papua*)¹ because this was the only species which occurred at all the localities visited. Observations on other species have been included where they seem appropriate, and my original field notes have been supplemented by observations on captive birds in various zoological gardens.

The life history of penguins has been studied by many authors. Nevertheless, no detailed analysis of their social behaviour had been attempted when we left England in 1934. Murphy's great monograph (1936) contains many stimulating ideas on this subject, but unfortunately, I was unable to see this until my observations were almost completed in 1937. Penguins are particularly suited for the study of intricate details of behaviour, because being almost without fear of man, they react towards one another in a perfectly normal manner, despite a human observer only 10 or 20 feet away. Furthermore, very large numbers congregate together during the breeding season, and they are birds of highly instinctive² behaviour which expresses itself in relatively simple patterns.

¹ Plate III.

² Using a definition of Allee (1939): "An instinct is a complicated reaction which an animal gives when it reacts as a whole and as a representative of a species rather than as an individual, which is not improved by experience, and which has an end or purpose of which the animal cannot be aware."

There has been a strong tendency to anthropomorphic writing, and the lack of exact knowledge is clearly shown by the conflicting accounts which have appeared. In this paper, a subjective and analytical method has been used. Simple description of the behaviour of penguins soon leads to an accumulation of notes that is quite overwhelming. The assumption was therefore made that behaviour can be resolved into simple component trains of actions, and the observations were made, from the beginning, with this in mind. The objective method of accumulating facts without selection was very soon discarded after a little experience.

The field work developed along four general lines, which may be briefly stated as follows:

1. Definition of the most characteristic actions which are constantly repeated, and investigation of the end to which each individual action leads.
2. Collection of information on the powers of perception of penguins in a preliminary attempt to discover which features of the environment cause them to respond.
3. Experiments to determine how much the normal stereotyped behaviour can be adapted to altered circumstances when a penguin is confronted with an unusual situation.
4. Observations to discover at what stages in the reproductive cycle the different activities begin, reach their peak, and end.

The whole enquiry aimed at furthering our understanding of the responses which birds make to external (exteroceptive) and to internal (proprioceptive) stimulation.

The characteristic succession of behaviour phases must, as Howard (1929) and others have supposed, be related to physiological changes; but little work has yet been done to correlate behaviour in the field with endocrine factors studied in the laboratory. Each new phase in the chain of events during the breeding season follows the last in a fairly orderly sequence. Each brings its own set of associations and starts a new series of actions which are performed mechanically. That most of these actions are habitual, not spontaneous, is shown by the regularity with which the same procedure is invariably repeated.

Certain glands elaborate hormones which appear to differ either in composition or quantity with the successive phases of the cycle of courtship, pairing, nest-building, laying of eggs, incubation and care of the young. These hormones have specific effects which, with the exception of structural changes, do not last unless more hormone is produced. Marshall (1936) has produced an invaluable summary of recent work on this, a subject which still remains obscure. It has been established that the anterior lobe of the pituitary is in some way stimulated through the inter-mediation of the nervous system to produce gonad-stimulating hormones, and in turn the gonads secrete hormones which act upon the accessory organs and tissues concerned in the sexual cycle, initiating the growth of secondary sexual characters, and also those phases of behaviour which are characteristic of the breeding season. The periodicity of the gonads is known to be partly inherent, but it is greatly influenced by environmental factors such as seasonal and climatic conditions, and by exteroceptive factors

dependent on the birds themselves, such as the stimuli of sight, hearing or sexual contact. There is now considerable evidence to support the assumption that the control of the internal secretion of the testis rests essentially upon a control of the activity of the pituitary gland; that conditions which modify pituitary activity likewise modify testis hormone secretion; and that a reciprocal influence exists between these two organs. But the precise environmental factors which influence the activity of the pituitary, causing it to regulate the onset of the breeding cycle, are for the most part still problematical.

The following discussion must be taken as a partial analysis of some of the observations which have been recorded. A study of this nature involves the collection of a huge mass of disconnected field notes from which it is possible to publish only those facts which seem most important. I am aware of the apparent inconsistencies and even contradictions in the following pages, but it is hoped that the method of presentation will allow reinterpretation of the original observations, and that the discussion will suggest further lines of approach.

CLASSIFICATION OF THE PENGUINS

The Penguins comprise one of the most well-marked major groups of birds. Their structural features are so distinct from those of other avian groups that in the opinion of some systematists they represent a sub-class of the class Aves, descended directly from the generalized primitive bird, and ultra-specialized as swimmers and divers. The discovery of about twenty fossil genera (Lambrecht, 1933) shows that they were circumpolar in the sub-Antarctic regions during early Tertiary times. From the present evidence of fossil remains, it seems clear that Miocene penguins had already specialized as swimming birds to very nearly the same degree as Recent penguins, and that their past distribution was much the same as it is at the present time.

Until recent years there has been very great confusion regarding the identity of the various species. The synonymy is extremely involved, and both scientific and common names have been wrongly applied. The following list of existing penguins is based on a critical survey of the literature and examination of skins in the British Museum. No attempt has been made to deal with subspecies of which a large number have been described. The division into families is new, and the arrangement is based on a consideration of behaviour, ecological relationships, and functional characters,¹ as well as morphology. The existence of fundamentally the same behaviour patterns among the strongly differentiated, widely distributed, members of the same Family, and their development with structure, indicates that these are as much a part of its evolution as form. Although the Latin names are perhaps less familiar than the English ones, they have been used throughout the succeeding pages wherever it is desired to bring out the functional affinities between the different families, genera and species.

¹ I have used the term "functional characters" to refer not only to characteristics of physiology and behaviour, but also to any characters which do not readily come under the heading of morphology, e.g., distribution and migration, type of nest and nest site, size of clutch, method of incubating, incubation and fledging periods, display attitudes, calls, care of young, moult sequence, method of progression, food and feeding habits, age at sexual maturity, affinities of parasites, etc.

ORDER SPHENISCIFORMES

(With known breeding localities)

Family EUDYPTULIDAE:

- Eudyptula minor* J. R. Forster Blue Penguin.
New Zealand, Stewart Island, Chatham Islands, Islands off the coast of Australia from Rockingham (Western Australia) to the Solitary Islands (New South Wales), and Tasmania.
- Eudyptula albosignata* Finsch White-flipped Penguin.
Banks Peninsula of South Island, New Zealand.

Family SPHENISCIDAE:

- Spheniscus demersus* (Linné.) Black-footed Penguin.
Islands off the South African coast from Angra Pequena to Algoa Bay.
- Spheniscus humboldti* Meyen Peruvian Penguin.
West coast of South America from Tierra del Fuego, north to Payta, Peru.
- Spheniscus magellanicus* (J. R. Forster) Magellan Penguin.
Tierra del Fuego, Staten Island, Falkland Islands, and coast of Chile to Mocha Island.
- Spheniscus mendiculus* Sundevall Galapagos Penguin.
Galapagos Archipelago.

Family EUDYPTIDAE:

- Eudyptes pachyrhynchus* G. R. Gray Thick-billed Penguin.
Coasts of New Zealand, Stewart Island, and Snares.
- Eudyptes sclateri* Buller Sclater Penguin.
Auckland and Bounty Islands.
- Eudyptes cristatus* (Miller) Rockhopper Penguin.
Tierra del Fuego, Staten Island, Falkland Islands, Tristan da Cunha, Gough, Prince Edward, Crozet, Kerguelen, Heard, St. Paul, Amsterdam, Campbell, Antipodes, and Snares Islands.
- Eudyptes (Catadyptes) chrysolophus* Brandt Macaroni Penguin.
Falkland Islands, South Georgia, South Shetland, South Sandwich, South Orkney, Bouvet, Prince Edward, Kerguelen, and Heard Islands.
- Eudyptes (Catadyptes) schlegeli* Finsch Royal Penguin.
Macquarie Island.

Family MEGADYPTIDAE:

- Megadyptes antipodes* (Hombron & Jaquinot) Yellow-eyed Penguin.
Otago Peninsula of South Island, New Zealand; Stewart Island, Auckland and Campbell Islands.

Family PYGOSCELIDAE:

- Pygoscelis papua* (Forster) Gentoo Penguin.
Staten Island, Falkland Islands, South Georgia, South Sandwich Islands, South Orkney Islands, Graham Land, South Shetland Islands, Prince Edward, Crozet, Kerguelen, Heard, and Macquarie Islands.
- Pygoscelis antarctica* (Forster) Ringed Penguin.
Graham Land, South Shetland Islands, South Sandwich Islands, South Orkney Islands, and Bouvet Island.
- Pucheranphus adeliae* (Hombron & Jacquinot) Adélie Penguin.
Coasts of Antarctica, South Shetland Islands, South Orkney Islands, and Bouvet Island.

Family APTENODYTIDAE:

- Aptenodytes patagonica* Miller King Penguin.
Tierra del Fuego, Staten Island, South Georgia, South Sandwich Islands, Prince Edward, Crozet, Heard, Kerguelen, and Macquarie Islands.
- Aptenodytes forsteri* G. R. Gray Emperor Penguin.
Antarctica: Cape Crozier, Haswell Island, Gaussberg, and Caird Coast.

NOTES ON NOMENCLATURE

Pucheramphus adeliae

Unfortunately, a matter of page priority necessitates the substitution of *Pucheramphus* Mathews for *Dasyrhamphus* Pucheran (Mathews: Bull. B.O.C., LV, 1935, p. 112). The type is *Catarrhactes adeliae* Hombron and Jacquinot. Most authors have included this species in the genus *Pygoscelis* Wagler, but I am in agreement with R. A. Falla that its bill and plumage characters warrant generic distinction from *P. papua* which is the type species of *Pygoscelis*.

Sub-genus *Catadyptes*

The genus *Catadyptes* Mathews (Bull. B.O.C., LV, 1934, p. 74) was described as "somewhat like *Eudyptes*, but with 14 tail feathers, not 16. A naked, somewhat tumid space at the base of the beak, which is of a light pink colour. The crest differs in construction in that it spreads across the forehead and joins the opposite crest. In *Eudyptes* the crest on each side is quite distinct." Adult specimens of *E. chrysolophus* which I have examined have 11 to 16 tail feathers, while *E. cristatus* has 11 to 14. *E. schlegeli* has a very limited tumid space at the base of the beak, but the marked differences in crest structure would seem to justify the retention of *Catadyptes* as a sub-genus for *E. chrysolophus* and *E. schlegeli*.

Pygoscelis antarctica

The genus *Dasycelis* was founded by Mathews (Bull. B.O.C., LV, 1934, p. 74) with *Aptenodytes antarctica* Forster as type. Mathews claimed that *Dasycelis* has 12 tail feathers in the adult stage, while *Dasyrhamphus* has 14 and *Pygoscelis* 16. This character is extremely variable and is valueless from a taxonomic point of view. A series of adult breeding specimens of *papua* which I have examined had 14 to 18 tail feathers, while *antarctica* had 11 to 14, and *adeliae* 12 to 17. The name *Dasycelis* remains available if it should be decided that the bill characters warrant a generic or sub-generic distinction between *antarctica* and *papua*, but these two species have very close functional affinities.

ARRIVAL AT THE COLONY AND FIRST MANIFESTATIONS OF SEXUAL BEHAVIOUR

The main features of the life cycle of *Pygoscelis papua* have been described by Bagshawe (1938). I was unable to make any extended observations in a rookery of this species during the very earliest period of the breeding season, and I am therefore particularly grateful to Mr. Bagshawe for the loan of all the original field notes which he made in Graham Land in 1921. The following information about the period before laying is based partly on his notes which cover this period in considerable detail.

In Graham Land, *Pygoscelis papua* makes only a partial migration during the winter. In the Falkland Islands the birds remain in the vicinity of the colonies throughout the year, and it is only in the southern part of their range that ice conditions usually compel them to leave the coast soon after the autumn moult. According to the state of the ice, they make occasional visits to the colonies either singly or in small parties, and wherever there is open water they may be seen fishing. In West Graham Land the colonies are partially reoccupied during August and the beginning of September. Parties of birds come ashore, usually in the morning, and stand about, singly or in groups, for hours on end, either sleeping or preening. No sexual activities take place, and there is no quarrelling. Gradually the numbers increase and the birds spend more time ashore at their old nesting grounds. There is nothing in their behaviour at this time to suggest that they are already formed into pairs.

At this stage, the nesting grounds in Graham Land and South Georgia are still covered with snow (Plate III, fig. 2). Long before it has melted away there are active signs of the coming nesting season. Much crowing goes on. There is a tendency for birds to separate out into pairs, and these bow and call to each other. Many of them take up positions where the rocks have become exposed, and, both here and on the bare snow, individuals may be seen bowing repeatedly, even if they are unaccompanied by another bird. The colony daily becomes the scene of greater

activity. To a human observer, certain features stand out because he sees them repeated time after time on every side. Some birds make depressions in the snow which serve as makeshift nests. Others may be seen carrying about pebbles or stems of Tussock grass and arranging them roughly in the form of a nest. Fresh pebbles are brought up from the beach and carried about for a time, then dropped, or offered to another bird which may be standing by an old nest site. Fighting becomes a regular feature of the colony. As the snow disappears, the nest sites provide circumscribed areas of great emotional valency,¹ and display becomes confined almost entirely to these areas.

Determination of the sexual relationships of the birds in a large colony is one of the most difficult problems connected with the study of their lives, and this is especially so with species like penguins which show no appreciable sexual dimorphism. Much has been written about the sexual behaviour of penguins, but most of these observations are of little value because the sex of the individuals described has been open to doubt. Behaviour gives no certain indication of sex, and even birds which have been marked immediately after copulating may easily be assigned the wrong sex owing to their habit of adopting reversed positions (see p. 208). In every case where the sex is stated in this paper, it was determined by dissection. My method was to mark² the individuals whose behaviour was being watched, and afterwards to kill them for examination. It was found best to use different combinations of coloured spots on the breast plumage, rather than to paint the actual field-book numbers on the birds. Whenever possible, all the birds in a small section of a rookery were marked and then left to settle down for a day before any observations were made. More frequently, however, it was only possible to make isolated visits to different rookeries, and on these occasions it was necessary to capture and kill individuals as the observations proceeded.

In 1935, ice conditions in Graham Land prevented any visits to penguin rookeries during the period which precedes egg laying. It was not until 9 October 1936 that I was able to visit a rookery at this stage. This was at Cooper Bay, in South Georgia, where there was a colony of about 2000 Gentoos. Thick snow was still lying over most of the coast, but the nesting sites were already largely snow-free due to the trampling of the birds. The majority were standing about alone, but occasional pairs occupied a nest. Many single birds were standing by old nests or carrying new material to add to them. On this and subsequent days a large number of Gentoo rookeries were visited, and observations were made almost every day until the eggs had been laid a fortnight later. Unfortunately it was not possible to confine these observations to a single rookery, but it was found that the first eggs were laid at approximately the same time in the different rookeries visited.

Tables I and II summarize typical observations on individual males and females. Corresponding notes on the measurements of their gonads are also given, and these will be considered in a later section of this paper where the relationship between the behaviour phases and gonadal development is discussed (pp. 226-29).

¹ The term "valency" was suggested by Russell (1934) as a substitute for "significance" or "meaningful stimulus" which can be given a teleological connotation.

² This was done with a special paint made for me in six colours by Messrs. Nobel Chemical Finishes, Ltd., who inform me that these products can now be obtained by reference to numbers 20083-20088: black, grey, blue, red, yellow, and green, respectively. I wish to acknowledge their gratuitous help in this matter.

TABLE I
PYGOSCELIS PAPUA: OBSERVATIONS ON MALES

No.	Date.	Locality.	Left testis.			Behaviour.
			Length mm.	Diam. mm.	Vol. cc.	
333	9.10.36	Cooper Bay.	39.5	18.0	6.7	Offering stones to ♂ A which made no response.
A.	"	"	14.0	6.5	.3	Occupying nest site: made no response to posturing and offering of pebbles by ♂ 333.
B.	"	"	20.0	9.5	.9	Occupying half completed nest: made no response to several birds which came to posture.
334	"	"	31.0	11.0	1.9	Immediately took possession of B's nest when B was removed and began to arrange nest material.
C.	"	"	21.5	9.0	.9	When 334 was removed this ♂ immediately re-occupied the nest and continued arranging the material.
D.	"	"	14.5	6.5	.3	Postured at me as I was sitting on the ground, but moved on after three bows.
335	"	"	48.5	21.5	11.7	Lying on empty nest with ♀ 336 standing beside him or occasionally bringing small bits of grass. He responded with vibrating movements of the flippers and slight lowering of his head each time.
F.	"	"	22.0	14.0	2.3	Arranging nest of tussock stems. Windy gusts blew material away as fast as he brought it, but this did not appear to affect his behaviour. Watched during 15 minutes making repeated journeys for grass, of which none remained in the nest. Few nests contained stones although there were plenty nearby.
G.	10.10.36	"	43.0	19.5	8.5	Arranging nest with ♀ to whom he made two bows accompanied by slight hisses. ♀ responded with two simultaneous bows. ♂ then started to nibble ¹ neck feathers of ♀, which lay down on nest with her bill and tail raised vertically. ♂ continued nibbling her neck feathers but gradually edged round until able to hop on to her back. He stood on the <i>middle</i> of her back with bill pointing downwards and overlapping her upturned bill. He remained in this position for about $\frac{1}{2}$ minute, nibbling round and round the feathers at the base of her bill and flapping his flippers to keep his balance. He made no attempt to move aft on her back, but hopped off and the ceremony was concluded by quick simultaneous bows.
H.	10.10.36	"	30.0	14.0	3.1	Offering grass stems to ♀ I, which was sitting on nest and responding by bowing and arranging the grass round her.
L.	"	"	26.0	14.0	2.7	Offering pebbles and bowing to ♀ K.
M.	"	"	29.0	10.0	1.5	Offering pebbles and bowing to ♂ N, which was sitting on nest but made no response. He repeated this once every 2 or 3 minutes until I interrupted him after 45 minutes. Seen pecking another bird of unknown sex.
N.	"	"	28.0	11.0	1.9	Sitting on nest and making no response to ♂ M, which was offering pebbles.
338	11.10.36	Undine S. Harb'r	42.0	18.0	7.1	Sitting alone on nest; not visited by any other bird during 45 minutes.
O.	"	"	39.0	16.0	5.2	Watched repeatedly bowing and hissing to an empty nest.
337	"	"	45.0	19.5	8.9	Made incomplected attempt to copulate with ♀. Behaviour similar to that of ♂ G.

¹ The bill is kept closed and vibrated.

TABLE II
PYGOSCELIS PAPUA: OBSERVATIONS ON FEMALES

No.	Date.	Locality.	Diam. of largest ovulemm.	Behaviour.
322	8.10.36	Grytviken	<5	Standing alone on shore, far from any rookery, at time when other birds were congregated at rookeries and actively engaged in courtship activities.
E.	9.10.36	Cooper Bay	16	Sitting on elaborate nest with another bird, taking material from an adjacent nest and laying it before her. Response invariably a <i>single</i> rather "half-hearted" bow.
336	"	"	18	Standing beside ♂ 335, which was lying on nest, and bringing nest material to him at intervals. Frightened away when ♂ was captured, but in 5 minutes she was back on the nest.
I.	10.10.36	"	8	Sitting on nest and arranging grass brought by ♂ H; responding to each of his visits with a single bow.
J.	"	"	5	Sitting on nest but making absolutely no response to ♂ which was bringing grass and laying it by her.
K.	"	"	19	Responding to ♂ L in the same way as ♀ I described above.
P.	"	"	9	Bringing grass to ♂ which was sitting on nest, and bowing to him.

These and other observations show that *in the early stages* the initiative in courtship may be taken by birds of either sex. The behaviour of an individual bird gives no indication of its sex, for the activities are interchangeable. Either the male or the female takes up a position in an old nest scoop, and it is not necessarily the opposite sex which then approaches to posture or offer nest material. There are two typical series of actions—one of initiation, the other of response. The bird occupying a nest scoop appears to be always the responding one; regardless of its sex. Presumably the sight of a bird sitting or standing in a scoop at this time releases an instinctive reaction in the way suggested by Lorenz (1935, 1937). The nest material is fetched and arranged by birds of both sexes—always in combination—since one collects while the other arranges. Were the nest to be left unprotected, the material would all be taken by neighbouring pairs. One bird bringing material evidently releases a behaviour mechanism in the other to arrange it in the nest. Thus two males or two females may go through the complementary actions together. It should be noted, however, that occasionally a bird occupying a nest scoop made no response to the posturing of another.

FIGHTING AND SEXUAL SELECTION

None of these observations suggests that the female *Pygoscelis papua* first secures a territory and then waits for the attentions of a male, as has been stated by Levick

(1914, 1915) for *Pucheramphus adéliae*. Gain (1914) ringed a number of *adéliae* and found that they returned to the same nest site the following year; but unfortunately no one has yet been able to ring penguins on a large scale and re-determine their sexual relationships the following season. It is not known whether a hen will mate with the same cock in successive years, but I believe that this must be a comparatively rare occurrence because of the many chances a bird has to get a new mate before its former mate returns. All the available observations go to show that none of the family *Pygoscelidae* arrive at their colonies already paired. It is possible, however, that individuals return to their old nest sites and that as a direct result of this the same pairs may mate in successive years.

Levick (1914) gives a good description of the fighting in a colony of *adéliae* but implies that the fights are between males competing for females. The fighting of *papua* is similar to that of *adéliae* (figs. 23 and 25), but it is less common and not nearly so fierce. It has already been well described by Bagshawe (1938). Skirmishes are very hard to unravel with assurance, but with *papua* I have records of opposite as well as like sexes fighting with each other. The females are less aggressive than the males.

Careful watch was kept for evidence of female choice. I could not find anything to suggest that the female of either *papua* or *adéliae* pays the slightest attention to the appearance of her mate, even if he is severely mutilated, with a foot missing. In the same way I could not find any direct evidence for sexual selection through the elimination of males which were unsuccessful in skirmishes with other males. Out of hundreds of fights watched, there were remarkably few in which it would have been possible to say definitely that one or other of the birds was the victor. It is usual for these fights to stop as suddenly as they have begun: just as if the combatants had suddenly lost interest in each other; but a territory-owning bird will often drive away intruders for some distance.

It is easy to demonstrate that a new mate is quickly found if one of a pair is killed, but more detailed experiments are required on the situation which thus arises. The only marked penguins which have remained under observation throughout the early spring were a few *adéliae* ringed by Gain, at Petermann Island on 29 October, a fortnight before the first eggs were laid. With these, the same pairs remained together throughout, and Levick himself recorded that pairs of marked *adéliae* remained together *after* the eggs had been laid.

None of the penguins seem to be promiscuous in the way implied by Levick and Bagshawe. A clearer distinction should be made between promiscuity as the normal state, in which both male and female have sexual intercourse with a number of individuals of the opposite sex taken at random, and promiscuity as an accessory phenomenon. In the latter case monogamy is the rule and only occasionally does one of the partners act unfaithfully.

To summarize: I do not believe that sexual fighting in *P. papua* or any other penguin brings about the regrouping of pairs (sexual selection in the Darwinian sense). Nor can we accept Howard's opinion that its only function is the securing of a territory, for it continues long after the eggs are laid, when all the territories have been established for some time. As Tinbergen (1936) and others have pointed out, sexual fighting in birds is never fighting under all circumstances, but it is always spatially

restricted. If fighting always occurs in the presence of some particular object, we must conclude that the fighting has the function of assuring its possession for the fighting bird. Levick's description of *adélieae* gives the impression that much fighting is quite independent of territory. But, except when a bird continued driving away an intruder beyond the territory boundary, in none of my penguin studies did I find instances of fighting outside the territory of one of the combatants. It should be made clear that in this case "territory" means the area immediately round the nest, (for a colonial bird may be just as territorial as a solitary one). In *papua*, fighting does not seem to be connected in any way with the presence of a temporary partner. The fights are between neighbours with adjoining territories, or with trespassers which come too near the nest. Any bird, of either sex, which comes too near will excite a territory-defending reaction. The mechanism by which this reaction is overcome in the case of mated birds is discussed later in the section on Social Organization (p. 214).

My experiments and observations all show great differences in the intensity of aggressiveness displayed by different individual birds. The external situation eliciting aggressive behaviour is not simply another penguin, but every other penguin which comes within the territory of a nesting bird. A penguin with eggs or young chicks appears full of courage, but if these are taken away even for a short time, the "courage" of the adult diminishes considerably. There is thus evidence to show that aggressive behaviour is partly controlled by visual stimuli which are effective only during a particular phase of the breeding cycle. The internal state promoting aggressiveness is apparently absent or so weak out of the breeding season that no fighting takes place.

Howard (1929) assumed that the territorial behaviour of birds was related to internal changes. There is now more definite evidence that aggressive behaviour in the breeding season is connected with endocrine activity. Evans (1937) measured the reaction time for isolated resident female lizards (*Anolis carolinensis*) to challenge non-resident female lizards placed in their cages. He found that ovariectomy profoundly altered this territorial response. The operated lizards reacted in a shorter time than controls with intact ovaries. Evans postulated that this was due to removal of a natural inhibiting effect which the ovarian hormones have on aggressive behaviour. Such a temporary suppression of the aggressive impulse provides a physiological framework for the rather surprising tolerance which adult penguins usually show to young birds.

Bird song and aggressive behaviour were first correlated by Howard (1929). Lack (1939) has shown that in the case of the Robin, song and aggressive behaviour occur in both sexes, and in autumn as well as spring. He therefore suggested that the gonadotropic hormones of the pituitary are responsible for aggressive behaviour rather than the sex hormones themselves. It is clear that aggressive behaviour depends not on one, but a complex of internal factors, pituitary and other glands acting and reacting upon each other. Once a certain (predisposing) stage of the cycle has been reached, these internal processes may be activated very rapidly by external stimuli.

In the case of *Pygoscelis papua*, experiments with a stuffed bird showed that aggressive behaviour weakens with the repetition of a similar external situation

producing it. The same thing was noted by Lack (1939) in his detailed study of the behaviour of the Robin. This is probably related to the known fact that prolonged use of certain of the hormones results in a progressively diminished response. After repeated injections of anterior pituitary hormone, for example, there is evidence that immunity results. (Collip, 1934).

Evidence that aggressive behaviour in penguins is not connected with conscious purpose is continually provided in any colony. A single example may be quoted from my field notes on *Eudyptes cristatus*. A female, which had not yet laid, was sitting on her nest with a male standing beside her. He attacked another male which approached, and the two birds fought round the sitting female for some minutes. Whenever *either* of them came within reach of her, she pecked at them indiscriminately and became raised to such a pitch of excitement that she even bit savagely at her own flippers. Such incidents as this make it difficult to believe that fighting brings about a change of partners or has any "selective" significance.

It is difficult to say precisely when two birds may first be considered as mated, but in most monogamous birds a pre-mating and post-mating period may be distinguished. Since the majority of "courtship" activities described in the literature occur during the post-mating period, they cannot be operative in any true form of sexual selection as understood by Darwin. Huxley (1923) has shown that in the Red-throated Diver the pre-mating as well as the post-mating ceremonies are definitely "mutual", in that both sexes play similar rôles. The courtship ceremonies of all the penguins which I have studied are essentially "mutual" in both the pre- and post-mating periods and this is also true of the Albatrosses (*Diomededidae*). There are remarkably few records of birds in which mutual display occurs in connexion with pair formation.

The view that sexual display and courtship serve to produce the necessary synchronization of male and female reproductive processes has been adopted by Howard and others. Marshall, however (1936), suggests a far more precise physiological signification. I cannot do better than quote his own words (p. 445): "It has been shown that the gonad-stimulating hormone of the pituitary will cause ovarian development and ovulation in birds, and that sexual posturing or even the mere association of two individuals will initiate nest building and ovulation. There is a presumption, therefore, that sexual posturing produces exteroceptive stimuli which act upon the anterior pituitary through the hypothalamus, and so effects the necessary synchronization between the sexual processes of the male and female birds. Herein then, in all probability, lies the biological or race-survival value of sexual display and of the adornment which in many species is taken advantage of to render the display the more effective. The birds which have brighter colours, more elaborate ornamentation, and a greater power of display must be supposed to possess a superior capacity for effecting by pituitary stimulation a close degree of physiological adjustment between the two sexes so as to bring about ovulation and the related processes at the most appropriate times." Upon the basis of this theory Marshall constructed a hypothesis comparable to Darwin's theory of sexual selection, but which encounters none of the main objections to which that theory is open. This idea of mutual selection gives display a definite purpose. It does not postulate that the female is influenced by the male so that she selects him, but suggests that it is the pair which

have the highest capacity for mutual stimulation which are most successful in perpetuating the race. For this process, Huxley's (1938B) term "epigamic selection" would seem to be more appropriate than Darwin's "sexual selection".

It is probable that in many cases the intensity of selective agencies may be extremely slight, yet still have an effect on evolution. In the penguins, the main selective component is presumably an indirect one; acting perhaps through an advantage gained from better nesting sites, or better utilization of the available breeding season. There is good evidence that both fighting and epigamic display may accelerate or retard the physiological processes of the breeding cycle.

BISEXUAL DISPLAY AND THE DEVELOPMENT OF DISTINCTIVE RÔLES IN EACH SEX

During the period before egg laying it is possible to trace the gradual development of sexual behaviour. Each day the Gentoos spend about 16 hours ashore, and they go off at night on the "massed fishing expeditions" which have been well described by Bagshawe (1938). These regular massed movements last for about a month, and it is during this period that copulation first takes place. Bagshawe gives several interesting tables which summarize his observations on the frequency of copulation at this time. His distinction between "complete" and "attempted or incomplete coition" shows clearly the way in which a large proportion of the earlier efforts are unsuccessful owing to unwillingness on the part of one of the birds.

In the same way much of the early display is incomplete or abnormal. Small frozen balls of snow may be used instead of pebbles for nest building; and birds will display in the absence of a mate. For example, in South Georgia a single cock Gentoos was observed standing alone. He suddenly began bowing repeatedly, and then mounted a small turf hummock, beating his flippers, with body arched and bill holding on to a tuft of grass. For half a minute he went through all the motions of copulation with the hummock. The ground was wet and it was not possible to determine whether any semen was ejaculated.¹ The behaviour of penguins displaying before humans must be placed in the same category. Several writers have recorded penguins laying pebbles at their feet, and I have watched them do this myself.

Howard (1929) has stressed this "confusion of impulses" which characterizes the early stages of courtship in all birds. He gives examples of the apparently aimless behaviour of Warblers (*Sylviidae*) and shows also that their first attempts at mating are abortive. For days on end in South Georgia the Gentoos were to be seen picking up stones only to drop them again, or collecting material in a scoop which was not subsequently occupied. But it is significant, as Howard has already pointed out, that this apparently aimless behaviour always follows a sequence having reference to the appropriate phase in the sexual cycle.

¹ Auto-erotism in birds, or the spontaneous manifestation of the sexual impulse in the absence of an external stimulus from another bird, has only rarely been recorded. Moll (1897) mentions that Parrots (*Psittacidae*) living in solitary confinement "masturbate" by rubbing the posterior part of the body against some object until ejaculation occurs. See also Selous (1902), who suggests that the Lapwing, when rolling on the ground and exerting pressure on the anal region, is moved by a "sexual impulse to satisfy desire". He adds that actual orgasm appears eventually to take place, a spasm of energy passing through the bird.

During this phase it is not uncommon to see behaviour such as that of male G (see Table I). The male scrambles on to the middle of the female's back and stands there helpless without attempting to complete the sexual act. He neither treads his feet nor makes any effort to reach backwards (fig. 17). Sometimes he does not even clasp the female's bill in his own. On 11 October, I found two females which had been fulfilling this active male rôle; the positions of the two sexes being reversed. Huxley (1914, 1923) has described this reversed pairing in the Great Crested Grebe, and has drawn attention to other cases in which both sexes play an almost similar rôle in courtship. In the Grebes, mutual display appears to attain the highest development yet described; the instincts of the sexes are so alike that successful coition evidently occurs both in the normal or in the reversed position. Either sex adopts the "active" or "passive" position according to circumstances. Bisexual or mutual display in birds seems to be not uncommon *after* a pair has mated, but very few cases of reversed attitudes in coition have yet been described (c.f. Selous, 1901, 1902; Whitman, 1919; and Tinbergen, 1931, who noted it in the Great Crested Grebe and Water-hen; Pigeon; and Common Tern respectively). In none of these could it be established with certainty that actual contact and transference of semen took place when the female was in the "active" position, and in most of them this definitely did not occur. Furthermore, it has now frequently been recorded that in the final phase of courtship before successful coition, the male often mounts the female without attempting to complete the sexual act. This has been observed by Selous (1901) in the Great Crested Grebe, by Howard (1929) in many different species of birds, by Tinbergen (1931) and Wachs (1933) in Terns, and by Tinbergen (1933) in Herring Gulls. In all these cases, as Howard expresses it, the reactions of the two birds were too low in intensity. Howard therefore says that in both sexes the impulse "waxes and wanes", and he assumes that posturing counteracts the waning of the impulse and in this way synchronizes the necessary actions of the partners. Howard (1929) and Darling (1938) also suggest that the action of the male in this preliminary mounting serves to stimulate the female to a state in which she will copulate. There is little doubt that it has this effect; but it also seems very probable that the phase of full sexual activity in the male has not yet been reached, and that the problematical hormonal secretions which we presume to be responsible for the active condition have not yet been produced in sufficient quantity. Howard's assertion that in the male bird all the reactions reach the required level rapidly and uniformly, so that he is fully prepared to respond when a female joins him, is not supported by my own observations on penguins. The male Gentoo acquires the ability to copulate as gradually as does the female, and a male which has once reached this stage may still fail to complete the act a few days later. A degree of sexual motivation which serves to excite a male to court a female and to bring her to a receptive state for copulation may still be much too weak to arouse the male to perform the copulatory act. It is also clear that the duration of what Howard calls the "prior sexual condition" or "pro-oestrus" in the female varies enormously in different species and different individuals.

After 12 October I was unable to visit another colony until the 20th, when activities were at a much more advanced stage. Very few birds were not paired and in possession of a nest site, and many pairs were observed in successful coition.

This almost invariably follows the same behaviour pattern. After the preliminary bows, the male starts vibrating his bill and stretches forward his flippers, patting the female with both of them, one on each side, urging her with bill and flippers to turn round and lie on the nest (fig. 15 shows the same behaviour in *Applenodytes patagonica*). He continues this patting throughout: his movements serve both to keep her in position and to maintain his own balance. Immediately after mounting, he reaches back, treading his feet and moving his tail from side to side until contact is effected. He bends forward so that his bill touches the upturned bill of the female. Both bills are rapidly vibrated throughout the act, but sometimes the female's bill is placed right inside that of the male; especially by *adéliae* (fig. 18). Immediately after ejaculation, the male slips quickly off her back again. The whole process lasts about 30 to 40 seconds.

During the previous week, the rôle of the sexes in display had been interchangeable, but now only the males were seen offering nest material to the females, while both sexes arranged the nests. Both sexes were still found sitting alone in nest scoops. From this date onwards I saw no case of a male standing only on the forepart of a female's back. Every mounting appeared to be followed by successful coition. The situation as regards "sex recognition" had also changed. Every active partner in coition which I examined now proved to be a male, and no female was seen to mount a male as during the previous week.

A light fall of fresh snow lay on the ground, so that the only uncovered pebbles were in the occupied nests. The males were to be seen constantly lifting pebbles from their own nests and putting them down again at the feet of their mates. Yet a strange male, which approached a female in the absence of her mate at this stage, was chased away even though he brought with him some tussock grass. It seems probable that the birds had not learned to distinguish the sexes as such, but that the birds of a pair, originally established by trial and error, had come to recognize each other personally. That individual birds learn to recognize each other in this way has been shown by Tinbergen (1936) with the Herring Gull, and by Noble, Wurm and Schmidt (1938) with the Black-crowned Night Heron, and many others.

The gradual development of distinctive male and female rôles is of particular interest. Goodale, Pézard, Zawadowsky and others (summarized by Marshall, 1922) have shown that the result of castration in the male and ovariectomy in the female is to produce a neutral type, which in the domestic fowl is much closer to the normal male than to the normal female. This work led to the idea of a neutral or indifferent type, upon which the internal secretions of the gonads operate and are responsible for initiating the growth of the distinctively male or female characteristics.

That the gonads are functionally correlated with the development of secondary sexual characters has long been known, but it is not yet known what precise cellular elements are responsible for the hormone which produces the development of the sex organs and psychological characters. The point of importance in connexion with penguins is this conception of the neutral type in birds as outwardly much nearer to the male than to the female.

At the beginning of the breeding season when the rôle of the sexes in courtship is interchangeable, the behaviour of *both* sexes approximates to that which is later followed by the male alone. The analogy suggests an explanation. It seems probable

that the hormones necessary for stimulating the characteristically female reactions in courtship are not elaborated until the birds are physiologically ready to receive the males. As already stated, both sexes go through the same activities during the early stages of courtship. It is only by "trial and error" that the males are able to recognize the females. Their subsequent behaviour is determined by the response which they receive from each bird to which their attentions are directed. So long as the females do not give a "female" reaction, they receive no more than spasmodic attention from the males.

The fact that ambisexual production of hormones is now known to take place—i.e. oestrogenic hormones from the testis and androgenic hormones from the ovary—is perhaps relevant in this connexion (Gallagher *et al*, 1937; Witschi and Miller, 1938, etc.). Elucidation of this problem must await further studies on the quantity and quality of the hormones actually circulating in the body.¹

SEX RECOGNITION

Display before a female Gentoo with unenlarged ovary fails to produce any response. But as her ovary matures, the stimulus provided by a male presumably helps to induce the secretion of hormones which determine her behaviour responses. It is clear with the Gentoo—and it is probably true of other penguins also—that in the first place the males make no discrimination between receptive and non-receptive females. But the attitude of a female in responding or failing to respond to the preliminary display of a male seems also to be of great importance in determining his subsequent behaviour. At an early stage, my observations in South Georgia led me to the conclusion that Gentoos do not discriminate between the sexes as such.

Several workers have made observations and experiments in connexion with this problem in birds. Whitman and his colleagues (1919) stated that Doves and Pigeons (*Columbidae*) do not know the differences between the sexes and that behaviour is the only guide they have in selecting a mate of the right sex. They reported numerous cases of individuals of the same sex copulating with each other. One or both members of a pair of females may assume the male attitude; and one may do so more frequently than the other, depending on the "relative masculinity" of the two birds. Females which are predominantly masculine with one mate may be predominantly feminine with a still more masculine mate.

In his study of the social life of birds, Schjelderup-Ebbe (1931) concluded that there is always a struggle for dominance between the two sexes, an assumption borne out in some species by the close similarity of the aposematic² or threat display used by the male when driving away an intruder and the epigamic display of the male when stimulating reproductive behaviour in the female. In this connexion Friedmann (1934) cites observations by Allen (1934) on the courtship of captive Ruffed Grouse in which the male seemed unable to distinguish between the sexes

¹ After the present paper was completed, a note by W. S. Bullough and R. Carrick has appeared in *Nature* (No. 3677, 20 April, 1940: 629). Following Witschi and Miller's proof that male hormone is produced by the female Starling and is demonstrated externally by a change in bill colour, these authors have shown that the development of male behaviour by the female in Autumn is concurrent with the development of yellow bill colour. A close correlation between a behaviour phase and hormone production has thus been established.

² The terminology used is that of Huxley (1938A).

(which are fairly similar, but not identical, in plumage). Speaking of the male, Friedmann writes: "It merely tries to intimidate one bird after another until it finds one easy to intimidate (usually a female). However, as some males come into breeding condition earlier than others and as a non-breeding male reacts to intimidation like a female, it sometimes happens that a male is made to be the passive, intimidated member of a 'pair' (of males)." Provided that one bird accepts a subservient position to the other, homosexual pairs may sometimes be formed during the breeding season. Such pairs have been found among Black-crowned Night Herons by Noble, Wurm and Schmidt (1938).

It was suggested by Allen (*loc. cit*) that "courtship display" is a form of intimidation in which the stronger bird, irrespective of sex, is the more active performer. Following up this idea, Friedmann urged that the need for intimidation in courtship is to guarantee the dominance of one sex over the other, and that the phylogenetic origin of courtship activities may have been in a type of mutual display practised by both sexes with consequent rivalry for dominance by one. But it is by no means universal in birds for the epigamic and aposematic, or intimidation, displays to be the same. The two displays are quite different in the Ruffed Grouse (Allen, 1934), Great Crested Grebe (Venables and Lack, 1936), Nuthatch (Venables, 1938), and Robin (Lack, 1939). They are also quite different in all the penguins which I have studied.

There seems to be little doubt that mounting behaviour in birds depends, at any rate partly, upon relative degrees of dominance, and it is possible, too, that the individuals of a pair may themselves vary from day to day in their mutual adjustments of dominance. The reversed pairing described in the last section may perhaps be partly due to varying adjustments of this nature. A cock Gentoo will copulate with a hen, but no sooner has he stepped to the ground than he may turn round and peck her. Such behaviour is easier to understand if it is considered in terms of dominance.

Recent experiments with stuffed specimens (Allen, 1934; Chapman, 1935; Noble and Vogt, 1935; Lack, 1939) have demonstrated the influence of threat and display characters in producing aggressive behaviour or courtship and the part which these play in sex recognition. The males of some dimorphic species clearly distinguish between the sexes on the basis of visual clues alone, but in others, even under natural conditions, a bird may not be able to select his own species with accuracy. It has also been shown that although a mated male may recognize his mate individually, he will copulate with a stuffed specimen. Lack's experiments with Robins, which will sometimes attack parts of stuffed specimens, show that the problem is not simply one of "recognition", but is very complex. In Pigeons (Whitman, 1919), Song Sparrows (Nice, 1937), and Red-necked Phalaropes (Tinbergen, 1935), there are no marked plumage differences in the two sexes. In these birds the sex of a strange individual is determined only by behaviour and calls, and a bird commences with similar behaviour towards all strange individuals.

After reading Chapman's paper (1935) on the courtship of Gould's Manakin, it occurred to me that similar experiments with penguins might be enlightening. Accordingly, a stuffed Gentoo was prepared with wires extending from the base of the feet, so that it could be made to stand in a life-like attitude in any desired position.

During December 1936 this bird was taken to a colony in the Falkland Islands at times when the birds were incubating eggs and brooding young.

Preliminary experiments showed that whereas they were unwilling to return to their nests when a strange object such as a hat or small wooden box was placed nearby, they showed absolutely no fear of the stuffed specimen. It was completely ignored unless placed within about 18 inches of the edge of an occupied nest. When placed on a nest containing eggs or young chicks, it almost invariably elicited the normal greeting bow and hiss from whichever of the two owners returned first. It was then attacked—presumably because it was unable to respond with similar behaviour. In very few cases did a returning bird not attack this specimen which was unable to make any response. On one occasion a female went through the customary greeting ceremony. She then pushed it aside and sat down on her eggs. For two or three minutes she vibrated her flippers, with lowered head, giving the normal female reaction to the attentions of a male. Then quite suddenly she stood up and began pecking the stuffed bird with such vigour that it was necessary to intervene to save the specimen.

Similar experiments with birds which were incubating fresh eggs usually gave the same result, but on several occasions males were seen to approach the specimen and lay grass or twigs at its feet. Unfortunately, there was no opportunity to test any birds during the period before laying, but it is suggested that a stuffed specimen would probably be ineffective in producing copulatory behaviour, for the male waits for certain movements and calls from the female to release his response.

The responses elicited by the stuffed specimen provided additional evidence that behaviour is the only guide which penguins have in selecting a mate of the right sex. It is therefore concluded that the formation of pairs results from "trial and error" advances on the part of one of the birds. Although the sexual impulse may be stimulated to some extent by the advances of a potential mate, the choice of any bird will thus be limited to those of the opposite sex whose sexual periodicity is synchronous, or comes as a result of display to be synchronous, with its own. This point is more clearly illustrated by the King Penguin which moults before breeding. From his observations in the Edinburgh Zoological Park, Gillespie (1932) has shown that the choice of an individual is limited to birds of the opposite sex which have completed the moult at about the same time. However, his contention that the female does the selecting requires confirmation.¹ Murphy (1936) quotes a letter from Gillespie who watched: "(1) a female pursuing a male and assuming male behaviour; (2) one male endeavouring to mate with another, even though a female was present and apparently receptive; and (3) two females attempting to mate, although an unmated male was with them." It should be added that Whitman (1919) first suggested that sex discrimination in birds of which the sexes are similar is affected by "trial and error" in the way described. My own conclusions were reached independently before returning to England in 1937.

Just as a male Gentoo is unaware of sex differences and does not differentiate between males and females even in mating, so is a female normally unaware of sex, and attempts to dominate weaker birds. The essential difference in the behaviour

¹ In a letter dated 2 November 1938, Mr. Gillespie informs me that in 1932 he had no really satisfactory means of knowing the sex of individual birds, and that he is now not so certain of this.

of the sexes is that during the breeding season a male always tries to dominate weaker birds, while a female loses this dominating urge during the short period when fertilization must take place.

SOCIAL ORGANIZATION AND THE FUNCTION OF SOME ALLÆSTHETIC CHARACTERS

There can be no doubt that some type of social order exists in a penguin rookery, but this is largely obscured by territorial habits. The continued stealing of nest material has already been mentioned. It is usual for such stealing to be resisted strongly, but occasionally a sitting bird allows its nest material to be removed without any resistance. For example, in South Georgia I watched a cock Gentoo collecting Tussock grass which was removed from his hen by a neighbouring cock as soon as he went away each time. The hen ran away a few feet every time this cock approached, giving indications of fear. In another case where the birds concerned were afterwards sexed, a male was "dominating" another male. Several other incidents of this nature were observed but the sex of the birds was not determined.

This is comparable with the "pecking order" in a flock of domestic fowls first described by Schjelderup-Ebbe (1922, 1931), and the "dominance hierarchy" which Masure and Allee (1933, 1934) and Murchison (1935) found to develop in groups of fowls. The establishment of such an order is based on a series of first combats and, once established, tends to remain constant. The social order is indicated by the giving and receiving of pecks, or by reaction to threats of pecking. When a pecking-order is fully developed, a dominant bird need only appear for the others to retreat without fighting. Allee (1939) and his colleagues have investigated the social order in a number of birds. Nearly all of these show a less rigid type of organization than is found in the domestic fowl. In most wild birds there is not the same absolute dominance of one bird by another. There is a pecking order, but social position is not fixed, and within a very short time reversals in dominance may take place.

The following example from my field notes is typical of the behaviour which has led to so much anthropomorphic writing about penguins:

In a colony of Gentoos at South Undine Harbour in South Georgia there were three nests—A, B, and C—forming the apices of a triangle about 4 feet apart. On B and C there were two birds, both of which proved to be males, each lying alone on well-made nests. A was an old scoop containing no pebbles. The bird on C got up and began to transfer pebbles from C to A at a rate of about three journeys a minute. The bird on B watched him, following every movement with his head; then went over to nest C; took a pebble during its owner's absence, and added it to his own nest. This was repeated many times, but frequently the bird from B was either early or late, and arrived at nest C at the same time as the rightful owner. On these occasions the bird from B stopped, looked aside, and gave every indication of having no interest in the matter until the owner of the nest had left with a pebble. He then waddled straight in and helped himself with great haste; in marked contrast to the slow

selection of the other bird. The important point to notice is that *whichever* of the two arrived first, the bird from B waited every time until the bird from C had gone. After about 10 minutes of this, the bird from C caught the "thief" taking a pebble and pecked at him viciously. The bird from B made absolutely no attempt to retaliate, but fled back to his own nest. I suggest that this behaviour was due to the fact that a pecking order had been established, and that such incidents give no proof of conscious purpose or intelligence.

Relative strength may be only one factor in the establishment of a pecking order. I was at first puzzled to find that a bird which one day appeared to be dominant in a group was not necessarily so a few days later. Then it became clear that the birds were far more aggressive when fighting close to their own nests than away from them, and it appeared that the exact location of an encounter between two birds might decide the subsequent order of dominance. Changes in the relative positions in the pecking order could thus be explained according to which was nearest to its nest when the two birds last met in conflict. On my return to England I was interested to find this phenomenon described by Lorenz (1938). Discussing the instinctive reactions which concern territory, he writes: "The chief characteristic of territory is the fact that any individual will fight with very much more vigour if the combat is decided in his own territory. . . . It has not been sufficiently emphasized that this increase of fighting power is not equal all over the ground defended by one individual bird, but that it always increases in proportion to how near a certain centre of the territory the fight takes place. . . . It is extremely prominent in the colony-nesting Herons (*Nycticorax*) because of the small size of their territories and the correspondingly rapid increase of fighting power which takes place when the bird moves a few yards from the outer boundary of his territory to its centre."

Lorenz' very illuminating paper on the comparative sociology of colonial-nesting birds suggested an explanation of the elaborate nest relief ceremony which is so well developed in penguins. Although their territorial reactions guaranteeing the immunity of the individual nests are not of the same order as in *Nycticorax*, the repeated bowing and hissing of the *Pygoscelidae* when one sex relieves the other at the nest seems analogous to the so-called "appeasing ceremony" of *Nycticorax*. To overcome the normal reaction to peck at any other bird which comes within striking distance, an "appeasing ceremony" has been developed which releases a greeting reaction in its place.

If a penguin occupying a nest is approached by its mate, it will tend to react aggressively in just the same way as it does towards a strange bird. Indeed, it is not uncommon to see one member of a pair peck at the other if the relieving bird arrives too suddenly at the nest because it has been attacked while passing close to other birds. The elaborate bowing and hissing of both sexes which accompanies the change over in incubation evidently prevents the birds belonging to the same nest from fighting each other (figs. 19 and 20). It is possibly quite distinct in function from the mutual bowing which occurs before the eggs are laid. Unfortunately, I did not appreciate this possibility while in the Antarctic, and my notes do not disclose any significant differences between the two ceremonies.

I have already mentioned that display sometimes occurs in the absence of other birds, but when bright colours or special structures such as plumes are rendered

specially prominent by the display action it is legitimate to postulate their evolution in relation to display. All such characters, which become effective via the sense-organs and brain of other organisms, have been termed allæsthetic by Huxley (1938A). These fall into two broad groups—those promoting inconspicuousness (cryptic), and those promoting conspicuousness (sematic). In the latter class are all characters concerned with threat and rivalry (aposematic), and display activities stimulating reproductive behaviour and the promotion of sexual union (epigamic).

As already noted, the movements in the epigamic and aposematic displays of *papua* are quite distinct, but the differences may be seen even more clearly in *adélieae* which has a more aggressive temperament. The aposematic display of *adélieae* is characterized by the erection of the feathers of the occipital crest (fig. 26). This erection also occurs when they are irritated by man (fig. 24). Sometimes it may be seen when two mated birds are displaying to each other before the eggs have been laid—when its function is presumably epigamic—but I believe that its appearance in photographs taken at this time of the season is often due to the close proximity of the photographer.

The function of the crests of the *Eudyptidae* is of special interest in view of recent suggestions concerning the ornamental plumes arising from the crown of the Night-Heron (*Nycticorax n. nycticorax*). According to Lorenz (1935, 1937) the greeting display of this bird illustrates his term “releaser” in an ideal manner, and he considers that the erection of the plumes serves, not for purposes of mutual stimulation, but to suppress a hostile repelling reaction which is otherwise natural to any Night-Heron approached by another. However, Noble, Wurm and Schmidt (1938) find no evidence for this interpretation in the American race *Nycticorax n. hoactli*. They state that the plumes are erected only during epigamic display and have no function in territory defence or in pacifying approaching individuals as reported by Lorenz. Furthermore, they claim that since the display of the male induces the female to gesture in the same manner, the performance is presumably stimulating to the latter. In *hoactli*, plugging the ears prevents a synchronization of greeting ceremonies, indicating that sound is more important than movement in calling forth the response.

In *Eudyptes cristatus* (fig. 12) the crown is covered with slender, glossy black plumes, increasing in length from the mid-line outwards, and is further adorned by lateral tufts of still longer yellow feathers, each of which has numerous straight, elongate, filamentous barbs. These yellow plumes form the free extensions of a sharply defined superciliary stripe, which begins above the gape about 5 mm. from the beak. My observations on this species do not justify any final conclusion as to the occasions when the crown plumes are erected—indeed, there does not seem to be any exclusive correlation between their erection and any particular phase of behaviour. Slight erection of the black occipital feathers certainly occurs in a wide variety of social situations, but the yellow superciliary plumes appear to be erected only during rage or fear.

At Tristan da Cunha, St. Paul and Gough Island, the breeding season is spread over a considerably longer period than at the more southerly colonies (see p. 231). At all the breeding localities, ovulation takes place about a month after the return from migration, but the birds are ashore from August to April in lats. 37°–40° S., and from October to April between lats. 49° and 56° S.

It is certainly interesting that the birds from Tristan,¹ St. Paul and Gough Island, tend to have much longer plumes than those from the more southerly localities. Measurements of the longest plumes from different breeding places are listed in Table III. The birds from the three northern islands have a massive crest with 40–70 yellow plumes on each side, while those from the southern islands have only 10–15 yellow plumes. The crests are certainly functional at other times than during the period before laying, and it would seem that we have here a possible demonstration of the evolution of a particular character correlated with the increased number of occasions upon which it may exert its selective influence each year.

TABLE III
MEASUREMENTS (mm.) OF LONGEST YELLOW SUPERCILIARY PLUMES AND LONGEST BLACK MEDIAL OCCIPITAL PLUMES OF *EUDYPTES CRISTATUS*

<i>Breeding Locality.</i>	<i>Yellow Superciliary Plumes.</i>	<i>Black Occipital Plumes.</i>
Tristan da Cunha	90 88 79	30 37 65
St. Paul	86 77	71 68
Gough Island	86	35
Crozet Islands	55 46	16 15
Kerguelen Islands	76 68 65 63	32 26 20 26
Falkland Islands	69 56 55 52	16 25 17 18
Campbell Island	77	21

It may be mentioned here that there is good experimental evidence that emotional excitement provokes an excess of adrenal secretion, and that excitement produces the same effects which follow the injection of adrenin (Cannon, 1929). This hormone has been synthesized, and when injected into the blood-stream of mammals it causes dilation of the pupils and the erection of certain body hairs. In a series of experiments to determine the action of adrenin on the muscles of the skin, Elliot (1905) found that the response varied directly with the functional use of the muscles. For example, a small injection of adrenin produced extreme erection of the

¹ Partly on account of differing crest development, Mathews and Iredale (Man. Bds. Austr. I. 1921, p. 11) divided *Eudyptes cristatus* into three subspecies: *moseleyi* from Tristan, *interjectus* from Kerguelen, and *filholi* from Campbell Island. In the opinion of the present writer the crests show a geographical variation which is worthy of subspecific rank, but no satisfactory grouping is possible until many more specimens have been collected from the different islands.

hairs on the tail of a Mongoose (*Herpestes mungo*). In the domestic hen, the only feathers erected were the small stiff ones constituting the eyebrow, but in a cockerel a similar injection was immediately followed by erection of the hackles at the back of the head and neck.

Although present evidence does not justify the conclusion that aggressive behaviour is caused by the increased secretion of adrenin, there are strong reasons for supposing that this hormone is directly responsible for certain epigamic and aposematic characteristics such as the erection of the crest feathers.

Further observations are required to elucidate the function of these brilliantly coloured superciliary plumes of the *Eudyptidae*. In *E. cristatus* and *E. schlegeli*, for example, it is perhaps significant that the plumes are very well developed in fully grown adults of both sexes, but are absent in the non-breeding yearlings. The adults apparently do not display to these yearlings. It is suggested that a profitable line of investigation would be to try the effect of cutting off the crests from all the adults in a small section of a colony at an early stage of the breeding season and then comparing developments with a neighbouring control group. Their behaviour should also be considered in relation to the histological condition of their gonads.

As Wilson (1907) has pointed out, it is in the head and neck that both generic and specific distinctive characters are specially developed in all the penguins. He adds that this is the only part which is visible for recognition when they are floating in the water. However, it is surely more important that it is the head and neck which are mainly concerned with the movements in posturing on land. In *Pygoscelis papua*, for example, the head is lowered to display the triangular white patches on the top of the crown (fig. 19). The movements of *Pucheranophus adéliae*, which has no special plumage characters on the head, are quite different (figs. 7 and 8). The somewhat similar display attitude of *Pygoscelis antarctica* differs only in that the head and neck are held vertically (figs. 9 and 10), exposing the black ring on the throat, instead of in the sloping position of *adéliae*. The bright superciliary plumes of the *Eudyptidae* are made prominent by rapid side-to-side movements of the head (fig. 12), and in *Spheniscus magellanicus* the heightened colour of the gape during the breeding season is correlated with repeated twisting of the head from side to side (fig. 16).

The epigamic and aposematic displays of adult *Spheniscus magellanicus* are apparently almost identical. During the breeding season all of the *Spheniscidae* are characterized by patches of bare, tumescent skin on the face. The feathers are moulted from the loreal space and in both sexes the exposed skin becomes highly coloured, forming a marked secondary sexual character. It is significant that in their yearling plumage, all the *Spheniscidae* are fully feathered on the loreal space, and this is again correlated with the fact that they do not breed until two years old.

Further examples of specialized head characters are unnecessary. The remainder of a penguin's body, even to the dark soles of its feet, which are turned upward while it is swimming, appears to be coloured and countershaded chiefly in conformity with the principles of low visibility under water.

The view that adaptive appearances have evolved in relation to the visual perceptions of birds and other animals is now supported by a great body of evidence (Cott, 1940; Huxley, 1938B). The arrangement of colour and pattern in the plumage of penguins provides a good illustration of the development of visual allæsthetic

characters capable of exerting an effect via the (distance) receptors of other creatures of the same or different species. It is of special interest that the epigamic and aposematic characters of penguins have developed in the head and neck, while the cryptic characters, which are only of value while the bird is in the water, have developed on the body.¹ On land, penguins have no enemies except man, but in the water they are attacked by seals. The Leopard Seal (*Hydrurga leptonyx*) feeds almost exclusively on penguins, and in the Falkland Islands the Sea Lion (*Otaria byronia*) frequently captures them.

TYPES OF DISPLAY IN PENGUINS

Behaviour patterns have been just as much subject to selection as has structure. The instinctive behaviour of penguins shows almost as much differentiation as does their morphology. Provided that behaviour patterns can be clearly defined, therefore, they should prove to be useful taxonomic characters which will help in the elucidation of their phylogeny.

At the present time it is only possible to indicate certain broad affinities, and for this purpose I have selected five well-defined behaviour patterns of social significance, which are worthy of further investigation:

(1). The use of pebbles, grass, and other objects during the early stages of the breeding cycle is particularly developed in the *Pygoscelidae* (figs. 13 and 14). When a bird brings a stone to the nest it lays the stone at the feet of its mate. The ceremony is usually followed by mutual bowing, and in the case of *papua* each bow is accompanied by a slight hiss (fig. 19). This behaviour is not exclusive to mated pairs at the nest site, but it appears to be confined to the breeding season.

The handling of nest material has also assumed a "symbolical" courtship significance in several other widely separated avian Orders (see Tinbergen, 1935; and references there quoted).

(2). Another type of posturing is also especially characteristic of the *Pygoscelidae*. Two birds standing together will bow very frequently to each other, or while one lies on the nest, the other will bow to it (fig. 19). In *papua* this bowing is especially developed and is invariably accompanied by the wheezing hiss mentioned in (1); both *adélie* and *antarctica* remain silent.

(3). The nest-relief ceremony has already been mentioned on p. 214. This occurs in slightly varying form in all the *Pygoscelidae*. In *papua* it is apparently similar to the posturing described in (2). Fig. 20 illustrates the stage following fig. 19, when the sitting bird has been induced to leave the eggs. In *adélie* the general pattern is similar, but there is more formality and less bowing. Instead of bowing on arrival, the relieving bird approaches with gracefully arched neck (fig. 21). The ceremony accompanying the exchange of the egg of *Aptenodytes patagonica* is also marked by repeated bowing, but in the other genera the movements appear to be different although equally elaborate.

(4). The mutual epigamic display of some of the penguins is very remarkable. It is perhaps most distinctive in *adélie* and *antarctica*. The two birds of a pair

¹ When wet, the yellow crests of the *Eudyptidae* cling to the head and become quite inconspicuous.

face each other with bills raised and sway their heads and necks alternately to right and left (figs. 7 to 10). The flippers are kept close to the body. This particular behaviour is confined to the pre-laying period, but it does not necessarily lead to copulation. It obviously has the function of mutual sexual stimulation. I have not seen this behaviour in *papua*, where it appears to be replaced by the bowing already described in (2).

The epigamic display of *Aptenodytes patagonica* is more varied than that of any of the *Pygoscelidae*. Standing opposite each other, the two birds of a pair open and close their bills very rapidly. Sometimes one of them makes a slight bow which is repeated by the other. Often they stand for long periods with bills crossed (fig. 11), and then one of them presses on the nape of the other until its head is bent almost to the ground. They "nibble" gently at each other's necks. The rapidity of the chattering movement of the mandibles is increased. The flippers of both birds begin to quiver and the tails to twitch. Finally, one of them may induce the other to lie down (fig. 15), and copulation ensues.

The mutual epigamic display of some of the other species of penguin has already been described on pp. 215–17. It may be noted here that the head swaying of the *Pygoscelidae* (except *P. papua*) is replaced in all of the *Spheniscidae* by a slow twisting movement of the head (fig. 16), while in the *Eudyptidae* there is evidently only a rapid turning of the head from side to side (fig. 12).

(5). The so-called "ecstatic" attitude of penguins has been described by many writers, but it does not seem to have been distinguished clearly from other types of display. This very characteristic attitude is shown in four different species in figs. 3 to 6. It occurs equally in both sexes of all the *Pygoscelidae*, *Aptenodytidae* and *Spheniscidae*, but has not yet been described in the *Eudyptulidae*, *Eudyptidae* or *Megadyptidae*.¹ The head is held vertically, with the neck elongated and the flippers raised horizontally or beating with slow rhythmic movements. This posture is usually maintained for 20 or 30 seconds. It is invariably associated with "crowing" (*Pygoscelis* and *Pucheranphus*), "braying" (*Spheniscus*), and "trumpeting" (*Aptenodytes*). The pattern is essentially the same in all the *Pygoscelidae* and *Spheniscidae*, but at its conclusion in *Aptenodytes patagonica*, the head is tilted forward with a jerk and the bird stands rigidly for a few moments before resuming other activities.

The call associated with the ecstatic attitude is infectious. If one bird starts, the call is immediately taken up by others until sometimes hundreds are calling together in the erect posture. The stimulus to this must be auditory rather than visual, for it can be communicated between separate groups some distance apart. Calls resulting from human intrusion may also start similar calls in an undisturbed group over 100 yards away.

The ecstatic attitude is seen most commonly at the rookeries during the breeding season, but it is frequently adopted by birds in the absence of their mates and sometimes by isolated birds away from their rookeries (especially *Spheniscus magellanicus*). More than any of the others, this type of display is often spontaneous in the sense that it may not be an immediate reaction to external stimuli. At the same time it rarely,

¹ Mr. L. E. Richdale tells me (*in litt.*) that *Eudyptes sclateri* twists and turns its neck during display, while *Megadyptes antipodes* "shoots its neck up very quickly, waits a moment with a sideways glance, and then lowers it. *Megadyptes* certainly puts its head to the sky like *adeliae*, but not for 20–30 seconds". It is to be hoped that the very detailed study of *Megadyptes* which Mr. Richdale is now making will clarify this matter.

if ever, leads directly to copulation. It is very doubtful if this particular "self-exhausting" display (Huxley, 1914) serves as "an emotional bond attaching the members of a pair". It is rather a type of social stimulation which presumably has an epigamic function for the whole community.

An exteroceptive, auditory stimulus usually initiates this posture, but since it often occurs without any apparent external element to stimulate it, there are reasons for supposing that it can be induced in the first place by a proprioceptive impulse. There is evidently a transition from an internal to an external stimulus which in turn intensifies the whole reaction. Southern (1938) has reached a somewhat similar conclusion in his study of the posturing of the Common Tern.

INCUBATION

The onset of broodiness in penguins is characterized by continued sitting on the empty nest. Before the eggs are laid, the birds usually leave their nests when disturbed, but later their impulse to run away from human intruders is so thoroughly inhibited that it is almost impossible to make them leave their nests even after the eggs have been taken. If they are thrown off their nests, they promptly return. They lose all fear of human beings, and are sometimes markedly pugnacious; at others, apparently lethargic. The intensity of the brooding instinct appears to vary considerably in different individuals, and it may disappear altogether in a very short time.

On 21 October, 1936, the first two eggs of the season were found in a Gentoo colony in South Georgia. The owners of these eggs were unwilling to leave them, but all the other birds in the neighbourhood fled on my approach. I took these eggs and put them in two other nests. The owners of these nests returned and immediately started to incubate as if there had been no change. After 30 minutes they showed no more unwillingness to leave than before and readily deserted the eggs when disturbed; but the owners of the eggs remained unwilling to leave their empty nests. One of these eggs was then placed in a third nest whose owner took no notice of it and remained standing beside the nest. All five of these birds were females.

An interesting demonstration of the strength of the brooding instinct was given by *Eudyptes cristatus* on Kidney Island in the Falklands. In December 1934, almost every bird in one colony had been robbed of successive clutches of eggs. Nevertheless, many of the nests were occupied by birds which were incubating either one or two stones which they must have collected themselves and which they were most unwilling to leave. On the other hand, those birds which were not brooding stones could be driven from their nests with comparatively little resistance.

The brooding habits of *Aptenodytes forsteri*, so well described by Wilson (1907), are even more remarkable. The egg is laid on the sea-ice and is then carried on the feet, loosely covered by a fold of abdominal skin. There is a much higher percentage of brooding than of reproducing adults. Every adult in the colony has a strong urge to incubate, and every time one of them relinquishes an egg or chick there is a "wild dash" of neighbouring birds to take possession. No great care is taken to save the egg or chick from injury, and the resulting mortality is considerable. Wilson also

records that it was not uncommon to see an old bird brooding a dead chick, or even a lump of dirty ice.

In common with *A. forsteri*, *A. patagonica* also develops a very strong brooding instinct. The characteristic incubation attitude of *patagonica* is shown in fig. 22. The bird is hunched up, with inturned toes, depressed tail, and a conspicuous transverse fold of skin covering the egg. Like *forsteri* they can move about slowly with short, clumsy steps, so that the egg remains on the metatarsi. When disturbed, they usually stretch upwards to their full height, but cling to their eggs even if driven along over rough ground. Murphy (1915) describes how in a colony in South Georgia some sealers gathered a heap of eggs together in one spot on the ground and that the robbed birds then visited the pile and appropriated eggs to replace their lost ones. I have myself seen them nursing smooth stones in place of eggs, and I can confirm Murphy's statement (1936) that if the egg is forcibly removed from the space between belly, tail, and feet, instead of rising immediately to the ordinary digitigrade gait, as they do after a normal exchange of the egg between mates, they shuffle around on the full length of the tarsi for about an hour. Willingness to part with the egg, and conditioning to an empty egg repository, evidently involves some complex internal change which is probably initiated by a visual stimulus during the relief ceremony. This is an interesting problem which would readily lend itself to experimental investigation.

That the egg itself supplies a visual or, more probably, a tactile stimulus, is further attested by Taibell's experiments with Turkeys (1928). He induced broodiness in a very short time by tying a cock bird down on to a nest of eggs. When the bird was removed, it immediately returned to incubate again. Another point may be mentioned in this connexion. For any one species the number of eggs in a clutch is generally constant. If some of the eggs are taken before the clutch is completed, it is usual for the bird to go on laying an indefinite number of eggs in an attempt to produce the normal clutch, the sight of which (or the touch) inhibits further laying. Apparently, reduction in the number of eggs is sufficient to stimulate the pituitary to put out follicle-stimulating hormone and the incubation phase is postponed in correlation with the repeated ovulation. Some species do not prolong their laying in this manner. In the *Procellariiformes* and *Columbiformes*, for example, the number of eggs is predetermined in the ovary, and they do not normally lay again at once if the first clutch is taken. So far as is known at present, all the penguins can be induced to replace eggs which are removed, but if stones are incubated instead, there is evidence, in the case of *Eudyptes cristatus* on Kidney Island, that the replacement interval is thereby increased considerably. Here again we have a problem which would not be difficult to investigate experimentally.

When we come to consider the physiological processes involved in the incubation instinct, there is more definite evidence upon which to base conclusions. Examination of *Pygoscelis papua* in South Georgia showed that the females began to sit about two days before the first egg was laid. Birds in this condition were found both before and after ovulation had occurred. That broodiness is not directly connected with the functioning of the oviduct has been demonstrated by cases in which it has occurred after the oviduct has been removed or put into a non-functioning condition (Pearl, 1914). It may be mentioned in this connexion that Riddle (1935) has extracted from

the anterior lobe a substance which is considered to be a distinct hormone. This substance, named prolactin, has been identified as the hormone primarily concerned in the induction of broody behaviour in the fowl. It has also been shown to cause the associated regression of the testis and ovary (Riddle, Bates, and Lahr, 1935). In a later paper (1937), these authors have shown that the pronounced anti-gonad action of prolactin is an indirect effect of its action on the bird's own pituitary, where it stops the release of follicle-stimulating hormone. This is of particular interest, since the purpose served by broody behaviour in female birds might otherwise be defeated by continued ovulation. The secretion of prolactin both inhibits ovulation and brings about the necessary synchronization of behaviour in the two sexes.

In all the species of penguins, it is known that both sexes take part in incubation. According to Levick (1915) the female *Pucheranphus adeliae* may not be relieved by her mate until a fortnight after she has laid, and the male then incubates for a similar period. This requires confirmation. More detailed observations on *Pygoscelis papua*, by Bagshawe (1938), are worth summarizing. Up to the laying of the first egg the male took spells of from 1 to 2 hours at a time to the female's 3 to 14 hours. Between the laying of the first egg and that of the second, spells of 5 to 15 hours at a stretch were taken in more or less equal proportion until the second egg was due to be laid. After the laying of the second egg, the spells lengthened to from 6 to 31 hours at a stretch. The interval between the laying of the first and second eggs was 77 hours. Out of a total of 336 hours during which one pair was watched, the female incubated for 183 hours and the male for 153. It is noteworthy that the male had the longest individual spell—of 31 hours.

The behaviour of *Eudyptes cristatus* is very different from this. In December 1936 the birds from 19 nests on Kidney Island were marked and observed for 10 days. Two females sat continuously throughout the whole of this period, 4 females sat for 9 days, 9 females sat for 6 days, and 2 females for 4 days, until relieved by their mates. During this time, 1 male sat for 3, and another for 4 days before their females returned. The share of the sexes is evidently somewhat similar in *Eudyptula minor*. Mr. E. W. Hursthouse, of Wellington, New Zealand, informs me that birds (of unknown sex) which he had under observation sat for periods of 5 and 13 consecutive days, but the latter seems to be unusual.

The incubation of a pair of *Spheniscus demersus*, in the London Zoo, was observed for me by Mr. A. White, to whom I am indebted for making a very detailed series of notes. The two sexes alternated irregularly in spells of between $\frac{1}{2}$ and $3\frac{1}{2}$ days. In this particular case the eggs were infertile and the birds continued to incubate closely until the 56th day. The normal incubation period is 41 days.

These examples are sufficient to demonstrate the wide variation in the different species of penguin. The present evidence does show, however, that some members of this Order incubate for exceptionally long periods without leaving the nest. In the present state of our knowledge it is scarcely profitable to do more than suggest that the alternation of the sexes in incubation and the varying periods taken by each are related in some way to an irregular secretion of a prolactin-like hormone. In some birds the alternation is so fixed in its regularity as to suggest an internal rhythm. I have described elsewhere (Roberts, 1940), the remarkably constant 2-day periods

of Wilson's Petrel and a similar regularity seems also to have been developed by some other petrels. The whole subject of the share of the sexes in incubation needs careful reviewing.

So far as they have yet been accurately determined, the incubation periods of penguins are listed in Table IV.

Levick gives an average of four observations to show that the interval between the laying of the first and second egg is 3.5 days in *adélieae*. Eleven records of *antarctica* by Bagshawe give an average of 3.4 days, and 7 of *papua* an average of 3.2 days. It is significant that the only time *papua* has yet been induced to breed in captivity (at the Edinburgh Zoological Park in 1937) the interval between the laying of the 2 eggs was 5 days. This was presumably a case of ovulation delayed by unfavourable environmental conditions. There is a 2-day interval in *S. demersus* which has bred frequently in England.

TABLE IV
INCUBATION PERIODS OF PENGUINS

* Personal communication

Species.	Days.			No. of Records	Authority.
	Max.	Min.	Average.		
<i>Eudyptula minor</i> ..	—	—	38	2	E. W. Hursthouse* (Wellington, New Zealand).
<i>Spheniscus demersus</i> ..	44	39	41.5	4	J. Fisher* (London Zoo) and Carl Hagenbeck* (Hamburg Zoo).
<i>Spheniscus magellicanus</i>	44	43	43.5	2	Carl Hagenbeck* (Hamburg Zoo).
<i>Spheniscus mendiculus</i>	42	39	41	3	L. L. Mowbray* (Bermuda Aquarium).
<i>Megadyptes antipodes</i>	50	40	?	many	L. E. Richdale* (Dunedin, New Zealand)
<i>Pygoscelis papua</i> ..	39	35	36.8	8	T. W. Bagshawe (1938).
<i>Pygoscelis antarctica</i> ..	40	34	37	15	T. W. Bagshawe (1938).
<i>Pucheranphus adélieae</i>	37	31	33.6	3	G. Murray Levick (1915).
<i>Aptenodytes patagonica</i>	55	51	52	6	T. H. Gillespie* (Edinburgh Zoo).

CARE OF THE YOUNG

It is surprising that for a time after the chicks hatch, brooding and feeding the young occur alternately, and yet these appear to be quite disconnected phases of behaviour so far as the stimuli which elicit them are concerned. When eggs are substituted for young chicks, an adult *Pygoscelis papua* will incubate them without apparent concern at the change. The adults do not seem capable of recognizing their own young, but if chicks about 2 weeks old are substituted for newly hatched young ones, the adults usually peck at them instead of sitting down to brood.

Once the young are able to leave their nests, they do not stray about regardless of territory like some colonial nesting birds. They bunch together in groups—the so-called “crêches” which have been described by several authors in the case of *P. adélieae*. This phenomenon occurs to a comparable degree in the other members of the *Pygoscelidae*, and it is even more developed in *A. patagonica*, where small separate

crèches are replaced by a single one which includes all the young of the colony (Pl. IV). In *A. forsteri* the system is quite different, though equally effective.

No comparable social system has yet been described in the other four families of penguins. Many adults, rather than just two parents, certainly do take turns in feeding the young, but the whole social system of a penguin colony at this time still requires detailed investigation. Young penguins do not seem to recognize their parents, or else their begging reactions are released on seeing any adult, so that they will molest every old bird they meet, crowding against it and trying to seize its bill.

The development of crèches is an interesting problem which does not seem to be confined exclusively to penguins. A somewhat similar, though less marked, habit occurs in the Sheld-duck, for where several pairs breed together, the broods unite to form packs with one pair of adults in attendance (Boase, 1938). The young of the Australian Pelican also bunch into mobs of from 10 to 40 or 50 when they are 4 or 5 weeks old (Macgillivray, 1923).

In the Antarctic species of penguin, the origin of these crèches may possibly be connected with the low environmental temperature. Kleiber and Winchester (1933) demonstrated that the huddling of chicks of the domestic fowl at low temperatures decreases their heat-loss by as much as 15 per cent, and they concluded that such huddling may be a means of saving energy. It has been suggested that the food requirements of the chicks is greater than can be met by one parent fishing alone, while the other remains ashore to protect the chicks. This may be true, but I have watched parties of Giant Petrels kill and disembowel young King Penguin chicks in a crèche while several adult penguins stood close by without making any attempt to interfere.

It may be mentioned here that Riddle and Dykshorn (1932) found that willingness on the part of doves to feed offspring which they had no part in incubating may be induced by injections of prolactin.

MOULT

The main features in the moult of only a few species of penguin have so far been described. In particular, reference may be made to the summarized information collected by Murphy (1936), and Falla (1937). The following papers also contain useful notes: Bartlett (1879), Cossar Ewart and Mackenzie (1917), Gillespie (1932), and Wilson (1907).

The moult will not be discussed in any detail here. It must, however, be considered in its proper relationship with the rest of the cycle, for most moulting phenomena are certainly due to hormonal influences (see references in Salomonsen, 1939¹). The close connexion between the moult and the breeding cycle is well demonstrated by certain birds in which the post-nuptial moult occurs prematurely when breeding is inhibited (e.g. the Fulmar Petrel: Wynne-Edwards, 1939). In *Aptenodytes patagonica* there is a very close connexion between the times of moulting

¹ Salomonsen considers emphatically that a thyroid hormone induces avian moults. But Miller (quoted by Witschi: *IX Congrès Ornithologique Internationale*, Rouen, 1938) has shown that the rise in thyroid activity observed in normally moulting birds is due to increased loss of heat by the partially depulmed bird. It is therefore a consequence, not the cause, of moulting.

and breeding, but in this case the moult is pre-nuptial. In spite of considerable variation in the date of moult, it appears to be followed immediately by pairing. The physiological processes involved are still unknown. Most of the penguins have a single post-nuptial moult which has a direct time-relationship with the varying dates of breeding in different latitudes, but there are some rather significant exceptions. In South Africa, for example, *Spheniscus demersus* has two peaks of egg-laying—in March and September. According to Kearton (1930), the majority moult between December and February, but many thousands do so before they have finished nesting, at a time when their consequent incapacitation renders them incapable of feeding their chicks.

Like the other phases in the cycle, the moulting time is characterized by marked changes in behaviour. In all penguins, the moult appears to be preceded by a period of unusually heavy feeding. During the moult itself, the birds stand motionless, sometimes for several days at a time. The whole process is marked by general lethargy, aversion to water, absence of appetite, laboured breathing, and absence of calling. The feathers are cast off in patches; not a few at a time as in other birds. The horny mandibular sheaths are normally shed at the same time as the feathers, but not always from both sides on the same day. Sometimes the bill fails to moult, so that there is an unsightly accumulation of horny material. This is especially noticeable in some of the captive *Spheniscus demersus* in the Edinburgh Zoological Park. Mr. T. H. Gillespie tells me that it is most marked in the oldest birds, one of which has been there for about 18 years, and has a particularly conspicuous mass of dead material adhering to its bill.

There is evidence to suggest that moulting may fail to take place in the absence of the appropriate environmental conditions. During visits to the Edinburgh Zoological Park in 1938 I was interested to find that a large proportion of the penguins¹ were in so-called isabelline plumage. Further investigation showed that all of these isabelline birds had failed to go through the annual moult, and that their coloration was due to fading of the pigment in the feathers. The longer the period since the last moult, the paler their plumage becomes. Eventually they moult straight from the isabelline plumage into the normal slaty-black one. Isabelline specimens of most of the penguins have now been recorded, but they are not common in the wild state, although there are many in museums owing to the custom of collecting anything abnormal. The brown plumage often met with at sea is merely the weathered state of the normal plumage from which the black has faded. The extraordinary bleaching power of the sun in the Antarctic is not sufficiently recognized as a cause of variation in plumage coloration.

SUMMARY OF THE BEHAVIOUR PHASES IN THE ANNUAL CYCLE

In the Gentoo, the annual cycle of behaviour phases may be summarized as follows: (1) Partial migration; (2) Visiting parties to the rookeries; (3) Partial reoccupation of rookeries and listless standing about; (4) Complete reoccupation of rookeries and adoption of territories; (5) Preliminaries to egg-laying such as display,

¹ Of three species: *Aptenodytes patagonica*, *Eudyptes chrysolophus* and *Pygoscelis papua*.

coition and nest-building; (6) Egg-laying; (7) Incubation; (8) Feeding and care of young; (9) Moults, and finally, partial migration again.

These behaviour phases sometimes grade into each other and slightly overlap, but usually each grows slowly to a climax and then abruptly ceases before the next phase begins to develop. It has already been remarked by several writers that when any disturbance interferes seriously with a bird's activities, it often tends to go back one stage in the sequence of activities and start again from that point. Thus, if the egg-laying stage is disturbed, the birds go back to nest-building. The sequence is sometimes broken. Incubation and sexual activity are mutually exclusive and antagonistic phenomena (see p. 222). Normally, copulation ceases immediately incubation begins, but I have a few records of copulation after the eggs have been laid, and one of apparently normal sexual intercourse between two Ringed Penguins which were feeding young about 10 days old.

ATTEMPTED CORRELATION OF THE BEHAVIOUR PHASES WITH GONADAL DEVELOPMENT

The gonads were collected and preserved from a number of representative Gentoo penguins whose behaviour appeared typical of particular phases in the cycle. Bouin's fixative was used on account of its general properties and the fact that material could be stored in it safely for long periods. The greatest length and diameter of the testes were measured, and the diameter of the largest ovule in each ovary. Part of each testis was later sectioned (8 to 10 μ thick), and stained with Delafield's haematoxylin and eosin.

It became clear at the very start that birds collected on any one day in the breeding season show considerable variation in the size of the gonads. It was also found that at this time the left testis is always larger than the right. (There were no exceptions to this in over a hundred cases examined during the breeding season.) This testicular asymmetry varies considerably; measurements of volume showed differences ranging between 1.3 to 1, and 4 to 1. Comparisons of sections of the two testes from several birds showed that both are equally functional as far as spermatogenetic activity is concerned, but apparently there are some differences in the amount of interstitial cells present in each. For the purposes of this discussion measurements and descriptions of the left testis only have been used.

Tables I and II at the beginning of this paper give some typical behaviour observations from 8 to 11 October—the period shortly before any eggs had been laid. In this table are also given the corresponding measurements of the testes and notes on their histology. The testis volumes are calculated on the assumption that each testis is an ellipsoid in which $a = \frac{1}{2}$ long axis, $b =$ semi-diameter at the largest part of the testis, and $V =$ the volume. The formula used is $V = \frac{4}{3}\pi ab^2$. The volumes of 22 of these testes were also measured by displacement in a graduated jar. The average error between measured and calculated volumes was 0.39 cc., the measured being slightly larger than the calculated in all but three cases. The measured volumes have not been used since only a small proportion of testes were preserved for this purpose, whereas linear measurements were made of all at the time of dissection.

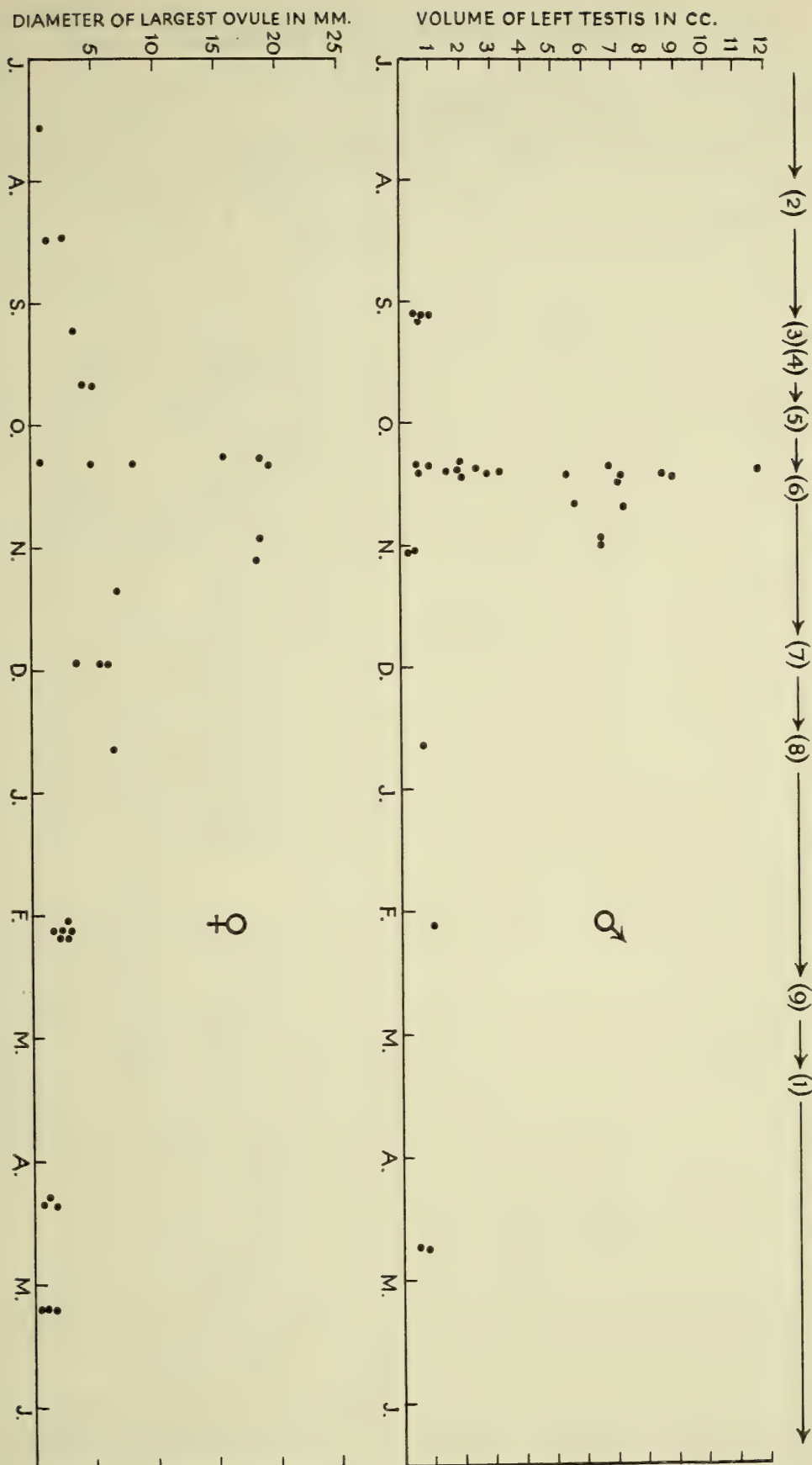


FIG. 1.—Seasonal gonadal changes in male and female *Pygoscelis papua*. The numbers in brackets indicate the approximate start of the behaviour phases summarized on pp. 225–26.

The number of specimens obtained out of the breeding season is small, but they are sufficient to demonstrate the main facts of the cycle. Fig. 1 illustrates the change in volume of the left testis of the males and the diameter of the largest ovule of the females at different times of the year. In the same figure the approximate dates of the beginning of each characteristic behaviour phase are indicated.

SEASONAL CHANGES IN THE TESTIS

The results of examination of twelve selected testis sections are summarized in Table V, and the main seasonal changes are shown in Figs. 27 to 34. The testes are smallest from early December until late September. In mid-October they rapidly increase in size to approximately ten times their previous volume. The greater part of this increase in volume is made up by increase in the diameter and contents of the seminiferous tubules. The actual volume of the testis, however, appears to bear no direct relation to the stage of development reached, for the kind and arrangement of the cells within the tubules may be similar in testes of widely differing volumes taken on the same day.

At South Georgia, free spermatozoa first appear in very small quantities at the beginning of October.¹ The awakening of copulatory ability is not coincident with the first appearance of free spermatozoa in the tubules of the testis. In several cases mature spermatozoa were found in the testes of birds which were as yet unable to complete the sexual act.² The period during which free spermatozoa are available lasts for at least 6 weeks, and extends from the time when nest material is being collected, until incubation is well advanced in the middle of November. None of the sections examined show complete inactivity, but by December there are no spermatids or later stages present in the testis.

Whether all the cells in the intertubular spaces may legitimately be called "interstitial" is open to question. There seems to be no agreement even amongst recent workers as to a correct definition of the term. They can readily be shown, by means of varied staining techniques, to be of more than one kind. Some of them are known to be secretory, and to these is usually attributed the production of the testicular hormones. It is not clear whether these interstitial cells are actually or only relatively fewer at the height of spermatogenesis, but according to Rowan and Batrawi (1939) the intertubular packing of most winter avian testes consists almost entirely of non-secreting, spindle-shaped connective-tissue cells with heavily staining nuclei, while in spring these give rise to secretory cells, possessing large and relatively conspicuous nuclei, rounded in shape and lightly staining.

In the sections under discussion, the diameter of the tubules is greatest at the height of spermatogenesis. There is no appreciable reduction in the number of tubules, nor a suppression of spermatogenesis during the early stages of incubation.

It may be concluded that the male Gentoo has a period of about 6 weeks during which it is possible for copulation to result in successful fertilization. However,

¹ Circumstances prevented the collection of specimens to determine the time when spermatogenesis begins.

² This is probably true of most birds, but copulation may also occur long before spermatogenesis is complete. Heinroth (1910) records that in the Mallard treading is regular from the end of September, although the gonads are not mature until December or later.

TABLE V
NOTES ON TESTIS SECTIONS FROM *PYGOSCELIS PAPUA*

No.	Locality.	Date.	Behaviour.	Volume of left testis (cc)	Approx. av. diam of tubules (μ)	Interstitial cells.	Kind and arrangement of cells within the tubules.
316	Stromness, S. Georgia	4.ix.36	Standing on beach far from colony.	·7	50	Small amount present, apparently somewhat compressed.	Many spermatocytes dividing but more mature stages absent. Lumen absent in nearly all tubules.
317	"	"	"	·4	60	More numerous, densely packed and completely filling intertubular spaces which are larger than in 316.	Many spermatocytes dividing but not so much activity as in 316. Most tubules have a distinct lumen partly filled with small numbers of degenerating cells.
333	Cooper Bay	9.x.36	Offering stones and grass to another ♂ which made no response	6·7	90	Interstitial tissue small in amount; does not fill intertubular spaces.	All stages to sperms with wavy tails, mostly held in clumps. Well defined lumen in nearly all tubules with small number of free spermatozoa.
334	"	"	Arranging nest material. No eggs.	1·9	100	More than in 333, but not completely filling intertubular spaces.	Not quite so advanced as 333, but all stages present. Very few free spermatozoa.
335	"	"	Lying on empty nest responding to attentions of ♀ with vibrating movements of flippers and slight lowering of head.	11·7	150	Slightly less intertubular space than 334, but about the same amount of interstitial cells.	All stages present. A few more free spermatozoa than in 334.
338	South Undine Harbour.	11.x.36	Sitting alone on nest without eggs.	7·1	130	About the same intertubular space as 334 but more interstitial cells.	All stages present. A few free spermatozoa, but most are held in groups round the tubule. Some tubules without a lumen yet containing all stages; others having small number of loose degenerating cells in the lumen.
337	"	"	Made incomplete attempt to copulate. Behaviour as ♂ G (Table I).	8·9	150	Slightly more than in 338.	Slightly more advanced than 335 and 338. Great nuclear activity in spermatocytes and many more spermatids than in 338, but about the same number of free spermatozoa. Some tubules without any lumen as in 338.
350	Bay of Islands	20.x.36	Watched copulating.	7·1	170	Apparently more than in 337.	All stages present with many more spermatozoa free in the lumen of most tubules.
353	St. Andrews Bay	28.x.36	Incubating fresh eggs.	6·4	130	About the same as 350.	About the same as 350.
518	Rabbit Cove, Falkland Is.	18.xii.36	With newly hatched chicks.	·6	50	Shrunk considerably but still plentiful. Intertubular spaces larger than in 350.	Most cells round the periphery of tubules are in a state of rest. A few spermatogonia show some activity. Lumen present in most tubules with sloughed-off degenerate cells in centre. No spermatids or later stages.
577	Port Lockroy.	3.ii.37	With chicks in second down.	1·0	50	Apparently less than in 518.	A few spermatogonia show some activity. Very few spermatocytes. Lumen present in most tubules with sloughed-off degenerate cells in centre.
282A	Rabbit Cove, Falkland Is.	18.iv.36	Just completed moult.	·5	40	Very small amount.	Advanced retrogression, but some signs of activity in a few spermatogonia. Very few spermatocytes. Tubules mainly full of debris.

copulatory behaviour is not subject to the condition of the testes alone, but is also partly dependent on appropriate stimuli from another bird.

SEASONAL CHANGES IN THE OVARY

The internal changes preceding ovulation in birds have been the subject of a considerable amount of research. Pearl and Boring (1918) found three kinds of structures in the ovary of a domestic fowl which had been actively laying: yolks of various sizes, indicating different stages of development, discharged follicles in various stages of regression, and atretic follicles or degenerating ova of different sizes. These are all easy to identify when they are large enough to protrude far from the surface of the ovary, but when they are under 2 or 3 mm. in diameter it is rarely possible to distinguish the remnants of the discharged follicle from the atretic. In earlier studies, Riddle (1910, 1916) showed that the growth of the yolks or oocytes is not a steady unbroken one; at a certain point there is a sudden increase to a rate about 25 times higher. In the domestic fowl, the transition from one rate to the other normally occurs when the oocytes have reached a diameter of about 6 mm., 5 to 8 days before ovulation. The transition is accompanied by a pronounced alteration in the type of substance accumulated in the ovum and in the growth and activity of the surrounding follicular membrane. A similar transition occurs normally in wild birds: notably the Starling (Bissonnette and Zujko, 1936). From the facts at present known, it is evident that this marked physiological change begins slightly earlier in larger birds than it does in small ones. Riddle and his colleagues (1927) have also demonstrated a remarkable series of changes associated with ovulation involving the thyroid, adrenals, parathyroids, oviduct and pituitary.

Howard (1929) first suggested that the change in rate of growth of the ovum might be physiologically correlated with nest-building behaviour, but no satisfactory investigation has yet been carried out to substantiate this view.

An ovary possessing a single well-advanced ovum may weigh considerably more than a more generally developed one without any far-advanced stages. For this reason, the best single standard of comparison between the sexual condition of different females seems to be the size or weight of the most advanced follicle in the ovary. Examination of a fairly large series of ovaries from female Gentoos captured shortly before egg-laying has given no indication of any marked behaviour phase correlated with the size of the most advanced follicle.

THE REGULATORY MECHANISMS OF THE REPRODUCTIVE CYCLE

It is now well established that in all the higher animals sexual periodicity, while conditioned by the environment, is regulated in its successive phases by the combined integrative action of the nervous and endocrine systems. It is evident that the phases within the cycle are brought into relation with seasonal environmental changes largely by exteroceptive stimuli among which must be included equally with the physical factors of the environment the psychical ones provided by the presence of another individual or the attitudes struck by a companion. The manner in which these stimuli play

upon the anterior pituitary and thereby effect changes in the inherent gonadal endocrine cycle varies greatly from species to species. (Marshall, 1936).

From my observations on the normal succession of phases in the reproductive cycle of penguins, and the experimental results obtained by other workers on birds, a tentative analysis can now be made of some of the internal and external factors which influence the time of breeding.

EXTEROCEPTIVE FACTORS

Of exteroceptive factors, attention has been mainly focused upon light. Experiments by many workers have demonstrated that it is possible by means of artificial illumination to induce normal recrudescence of the gonads during mid-winter; but the distinction between the breeding condition and actual breeding should be recognized more clearly than has often been the case.¹ Under natural conditions light is only one of the factors concerned in the determination of avian breeding seasons, and too much significance seems to have been attached to the influence of light as a single factor (Baker, 1939). It is the increase, not decrease, in duration or intensity of illumination that is known to stimulate reproduction. Consequently those birds which start to reproduce when the days are shortening present a special problem. Whereas most of the Antarctic penguins have fixed breeding seasons at the warmest and lightest time of the year, *Aptenodytes forsteri* lays at the beginning of July—in mid-winter—when it is quite dark. A similar phenomenon occurs in the Nelson Province of New Zealand, where the Kea also breeds in mid-winter, at a time when the weather is extremely severe (Marriner, 1909). In such cases it is possible that the birds are giving a delayed response to the increase of light earlier in the year (Baker, 1938).

Eudyptes cristatus has a wide breeding range which is circumpolar and extends through 19° of latitude. Table VI gives the facts as they are at present known and indicates a general correlation between latitude and breeding date. In view of recent experimental work, it seems probable that this correlation may be related more to local conditions than to rate of change of intensity of illumination in different latitudes. It is certain that length of day is not always the controlling factor; for example, some species of birds have quite different breeding seasons on the two sides of Ceylon (Baker, 1939). This conclusion is also borne out by the fact that during the Australasian Ornithologists Union's visit to the Capricorn Group in October 1910, the White-capped Noddies showed no sign of laying on North-West Island, whilst birds of the same species were laying in hundreds on Masthead Island, only 15 miles away. (Barrett, 1910).

On the islands off the South African coast the breeding season of *Spheniscus demersus* is very indefinite. The Superintendent of the Government Guano Islands tells me that a few may be found nesting at any time of the year, but that there are two periods of maximum laying: in March and September. Even these dates are subject to variation owing to unknown causes. On the Peruvian coast, *Spheniscus humboldti* also appears to have developed a wide flexibility of breeding season. Murphy (1936) has collected together the known breeding records, but these are insufficient

¹ e.g. Spermatogenesis or maturation of the ova does not necessarily lead to normal mating and the production of fertile eggs.

to show whether there is continuous breeding throughout the year or two distinct nesting seasons in April–May and October–November. Correlated with its more southerly distribution, the closely-related *Spheniscus magellanicus* has a single breeding season in November–January. *Spheniscus mendiculus*, the only tropical penguin, has only once been found nesting in the wild state in the Galapagos Islands (in March), but in captivity it has bred successfully in the Government Aquarium at Bermuda. Dr. L. L. Mowbray informs me (*in litt.*) that between 1935 and 1937 eggs have been laid in March, April, May, and December.

TABLE VI
DATES OF BREEDING SEASON OF *EUDYPTES CRISTATUS*

	Latitude S.	Arrival.	Eggs.	Moult.	Departure.
Tristan da Cunha	37°	Aug.	mid-Sept.	Feb.–Mar.	April.
St. Paul	39°	Aug.	Sept.	—	March.
Gough Island	40°	—	mid-Sept.	—	—
Kerguelen Islands	49°	early Nov.	Nov.–Dec.	Feb.	March.
Antipodes Island	50°	—	Nov.–Dec.	Feb.	—
Falkland Islands	52°	mid-Oct.	early Nov.	Mar.–Apr.	late April
Heard Island	53°	—	Nov.–Dec.	—	—
Campbell Island	53°	early Oct.	early Nov.	—	—
Macquarie Island	54°	mid-Oct.	Nov.	April.	late April.
Cape Horn region	56°	—	Nov.	—	—

Aptenodytes patagonica also shows considerable variation of breeding date. Reports from widely separated breeding stations in the sub-Antarctic indicate that, while the peak of egg-laying comes in November or December, eggs in every stage of incubation may be found at any locality between October and March. The moulting régime of *A. patagonica* shows a similar irregularity, for moulting adults have been noted during every month between November and April.

While the breeding seasons of many of the penguins are fixed within comparatively narrow limits in any one locality, there is thus reason to believe that some of them are largely free from external seasonal influences. In this respect they would seem to be almost unique among birds. It is suggested that *Spheniscus demersus* and *Aptenodytes patagonica* are the most suitable species for the further investigation of this problem, which is perhaps connected with the relationship of the breeding season to the moulting régime.

Before any further discussion of exteroceptive stimuli, it is necessary to review very briefly what is at present known of the sexual season in birds.

Howard (1935, 1939) postulated that male birds have a long annual period of sexual maturity and females a short one. Allen (1934) considered that the period

may be either longer or shorter in the male, and that it varies with species and individuals, especially with age. Lack (1939) suggested that the male Blackcock has a longer period of sexual maturity than the female. None of these writers examined the gonads of the birds which they were observing, and physiological data are therefore lacking.¹ Mainly as a result of his observations on the behaviour of Warblers, Howard (1935) has distinguished three phases in the reproductive cycle of a female bird; first "pro-oestrus" or a prolonged period during which there is much ineffective posturing, varying in intensity and frequency from day to day and in different individuals, but never leading up to copulation. This is followed by a short "oestrus" phase, when the female is willing to receive the male and builds in part; and finally, there is a third phase, when she finishes the nest and lays eggs, but loses sexual excitement.

It is thus generally assumed that female birds have a short but definite "oestrus" period when they are ready to copulate. There is certainly a limited period during which fertilization is possible, but it is equally certain that copulation occurs throughout a considerably longer period than is necessary for successful fertilization. Howard's adoption of the terms "pro-oestrus", "oestrus" and "anoestrus" are convenient, but require closer definition if they are to be used for birds in general. Pro-oestrus may be defined as the whole period from the time when overt sexual activity commences until successful copulation is first effected. This is followed by the oestrus phase which lasts only during the period when copulatory behaviour persists. Nest-building often takes place throughout the whole of oestrus and part of the other two phases, and since copulation sometimes continues after the eggs are laid,² it is unsatisfactory to say, as Howard does, that the nest is finished and the eggs are laid during a third and distinct phase. It is necessary to retain the term anoestrus for the period when all overt sexual activity is absent, and when there is no disposition to seek out a mate; for it was in this sense that Heape originally proposed it when describing the sexual processes of mammals.

The duration of these phases appears to vary considerably in individuals of the same species. On the same day two female Gentoos may react in different ways to the posturing of a male.³ One may take no notice while another responds actively until mutual stimulation leads to copulation. Sometimes copulation is preceded by prolonged posturing; at others it occurs without any preliminaries. One pair may be together for a fortnight; another for only a few days before the eggs are laid. But although the duration and intensity of courtship behaviour varies considerably from one individual to another, the first eggs in a rookery are all laid at about the same date.

The successful completion of the breeding cycle must depend on synchronization of the oestrus phase of the female with the period during which the male is capable of inseminating her. As already mentioned, this period was found to last about 6 weeks in the male Gentoos. It seems probable, however, that there is no fixed period of this nature in any species, for its duration is under variable endocrine control which is

¹ We are here concerned with wild birds which have a seasonal cycle. Birds show many types of normal testicular activity, from the strictly seasonal to the continuous spermatogenetic type. Those species rearing more than one brood have a correspondingly extended period of testicular activity.

² The Wandering Albatross continues to copulate regularly even after the young have hatched.

³ As appears to be the case with most birds, the intensity of reaction is higher in the early morning than later in the day.

in turn largely subject to external circumstances. The maturation of ova in the female and her oestrus phase are conditioned in the same way, and as far as synchronization is concerned, there is obviously a large safety margin which ensures that there shall be spermatozoa present in the oviduct when ovulation occurs.

We may now consider the processes which bring about ovulation. As Marshall (1936) has pointed out, the fact that eggs taken shortly after being laid are usually replaced after a brief interval, shows that the succession of phases is not merely a matter of cyclical endocrine control. Phillips and Warren (1937) conclude that ovulation is due, at least in part, to pressure resulting from the prolonged tension of the muscle fibres of the follicular membrane. The grasping of the follicle by the infundibulum is not a causative factor (Warren and Scott, 1935). The time of ovulation itself is probably regulated by the sequence of maturation of the ova.

The determination of the time of egg-laying does not necessarily depend on insemination by a male. Copulation is repeated so often at this time that it is difficult to say exactly when fertilization takes place, but it evidently occurs after the egg is set free from the ovary (Hartman, 1937). To judge from the interval between the laying of the two eggs in a clutch, the passage of the egg down the oviduct of a Gentoo probably takes about 70 hours. In the pigeon, neither copulation, nor the presence of spermatozoa in the oviduct is known to be essential to ovulation (Craig, 1911). In the domestic fowl fertility persists for about 15 days after removal of the cock (Walton and Whetham, 1933), so that temporary cessation of copulation cannot affect the time of ovulation. Such inhibition does appear to take place in penguins during periods of exceptionally bad weather, when snow is drifting, but not when the temperature is well below freezing in fine weather.

Though the time of ovulation is primarily dependent on the state of the ovary, it is immediately controlled by external circumstances acting through the nervous system. Some of these exteroceptive stimuli depend on the relations between the sexes, others on the physical environment. Certain exteroceptive factors definitely inhibit the completion of the normal cycle. It has long been known that ovulation in birds may be delayed in the absence of satisfactory nesting facilities (Harper, 1904; Lack, 1933) or if the birds are disturbed by anything occurring in the neighbourhood of the completed nest (Craig, 1913). A sudden cold spell may delay the completion of a clutch (Rowan, 1918). In connexion with this point it is interesting that Riddle and Honeywell (1924) found ovulation in pigeons to be normally associated with their capacity to effect a temporary increase of the blood sugar above its normal concentration, and that conditions which oppose this capacity tend to suppress ovulation. They also showed experimentally that prolonged exposure to air of strong cooling power results in a marked lowering of the concentration of the blood sugar of pigeons. In addition, Cannon and his colleagues (1929) have shown that emotional excitement is associated with a temporary increase of blood sugar.

The behaviour of penguins appears to vary with the state of the weather much less than is the case with most birds. In South Georgia, the Gentoos often continued to build their nests while snow was actually falling, and activities of this nature were only inhibited by a strong blizzard. It seems, also, that this cessation of activity was primarily due to the snow-covering over the available nest-material which is so inseparable from many of their actions at this time.

Bad ice conditions sometimes delay the whole breeding cycle. At South Georgia, the Gentoos began to lay about a fortnight earlier in 1936 than they did in the previous year. At the beginning of October 1935 there was heavy pack-ice all round the east end of the island and considerably more snow than usual. The penguins remained on the beaches and did not congregate in their rookeries until the ice had dispersed. That the state of the pack-ice may be an important factor controlling breeding time in some of the Antarctic penguins is also well demonstrated by the available records from Graham Land.

Aviculturists have long been aware that ovulation in birds is normally held in abeyance until the proper stimulus is received from a mate or companion. The mere presence of another individual provides an exteroceptive stimulus which starts the nest-building and ovulating stage of the cycle. In the case of Pigeons, it has been proved experimentally by Craig (1911, 1913) and by Matthews (1939) that this stimulus is visual, and not tactile, olfactory or auditory. Visual stimulation clearly plays a very important part in regulating the reproductive cycle in penguins. Some of their most distinctive attitudes have already been described (see pp. 218-20). Marshall (1936) concluded that such display in birds does not produce a conscious sexual selection as proposed by Darwin, but is essentially a mutual pituitary stimulation. This idea has been developed by Darling (1938), who suggests that the displays and social interactions of the members of a colony exert a cumulative stimulatory effect on the reproductive functions of the individuals which is necessary, or a factor of major importance, for successful breeding. His observations on Lesser Black-backed and Herring Gulls led him to conclude that a definite minimum number of pairs is a requisite in any breeding colony of certain colonial nesting species, in order to produce the threshold stimulus for ovulation. Darling found that in almost all cases that he examined the larger colonies not only started laying earlier, but the time taken by the whole colonies to lay their whole quota of eggs was shorter than in the smaller colonies.

Social stimulation of this type is clearly of varying importance in different species. A Gentoo colony may contain about 12,000 pairs, yet the peak of egg-laying is not reached, in spite of the presence of large numbers of birds, until more than a fortnight after the laying of the first egg (Bagshawe, 1938). The same thing was found to be true with the Rockhopper Penguins in the Falkland Islands, but it is significant that the first eggs were always laid at about the same time in the different colonies. A good test of the effect of different numbers of birds was given by a rough census of 137 Gentoo and Rockhopper Penguin Colonies made in the Falkland Islands in 1936. Although these ranged in size from 30 pairs to approximately 800,000 pairs, I was unable to find any conclusive evidence that laying started earlier in the largest colonies, or that ovulation in the large colonies was spread over a shorter period than in the small ones. In January 1935, a single pair of Gentoos was found nesting on an isolated promontory in the Palmer Archipelago, yet their chicks were at exactly the same stage of development as those in a colony of about 40 pairs a mile away. Most of the Graham Land Gentoo colonies were composed of a number of small groups of 30-40 pairs occupying neighbouring rock outcrops. In each of these groups, the chicks were at the same stage of development, yet the different groups sometimes varied in age by more than a week. It is also significant that in the King Penguin colonies of

South Georgia the different groups of breeding birds differed very widely in the stage of the breeding cycle reached, but all those in any one group were at approximately the same stage.¹

These observations suggest that the breeding time of penguins is under social control, but there seems to be no minimum threshold number of birds necessary to enable them to complete the cycle. There is little doubt that the female reacts to the situation as a whole: that the activities of nest building and contact with the nest combine with the stimuli of another bird or birds to accelerate the processes which bring about ovulation. The changes in the physical and psychical environments which may either promote or delay the successive phases of the breeding cycle are summarized tentatively in Table VII. These features refer particularly to the Gentoo Penguin, but are clearly of wider application.

TABLE VII

SOME EXTEROCEPTIVE FACTORS REGULATING THE BREEDING CYCLE PRIOR TO EGG-LAYING

<i>Promoting.</i>		<i>Delaying.</i>
PHYSICAL ENVIRONMENT		
Daily increase in duration or intensity of light.		Unsatisfactory nesting conditions caused by snow, flooding, etc.
Presence of satisfactory nesting conditions.		Late dispersal of sea-ice.
Early dispersal of sea-ice (in high latitudes).		Cold spell.
Period of warm weather.		
PSYCHICAL ENVIRONMENT		
Visual stimulus provided by mate.		
Social " " " communal display.		
Self " " " ecstatic attitude.		
Auditory " " " mate and other birds in the colony.		
High position in dominance hierarchy.		Disturbance of any kind.
Successful fighting.		Low position in dominance hierarchy.
Visual stimulus of nest-material and nest-building activity.		Unsuccessful fighting.

PROPRIOCEPTIVE FACTORS

It was stated earlier in the present section of this paper that the onset of sexual behaviour in both sexes is regulated by the combined integrative action of the nervous and endocrine systems. Some further evidence concerning endocrine control may now be mentioned.

Most of the experimental work so far carried out in this connexion has been concerned with the physiology of the sex glands and accessory organs, the biochemistry and assay of gonadal and gonadotropic hormones, and the inter-relationships of the various glands. Abundant evidence is available to show that the cyclical changes

¹ Evidence of a similar nature from a tropical area is contained in a paper by Hoogerwerf (1937). In West Java, the Black-headed Ibis breeds socially on platforms holding 20 to 25 nests. The eggs or young on one platform are all at a similar stage of development, but this is not necessarily the same as that on any other platform. Further cases are quoted by Lack and Emlen (1939).

in the structural secondary sexual characters are subject to hormonal control (see especially Allen, 1939, for a summary of recent work), but experiments as to the effects on *behaviour* of the removal or transplanting of certain glands, and of the injection of hormones, are still few in number.

The gonads of seasonal breeding birds are quite inactive during several months of the year, but numerous experiments have shown that by the injection of gonadotropic hormone they can be made to secrete hormones in quantity at any time of the year. As far as evidence is available, the stimulation of the testis and ovary to secrete hormones resides in the action of anterior pituitary gland secretions. Indirectly, therefore, the control of the gonadotropic activity of the pituitary must account in large measure for the regulation of gonad activity. It is also commonly believed that at least one factor in the control of pituitary secretions is the circulating gonad hormones.

Most birds exhibit a definite periodicity in hormone secretion which is indicated by their own typical secondary sex character responses. There is general agreement among investigators that such characteristics as voice, courtship behaviour and pugnacity are affected by castration, and are therefore dependent for their expression on hormones. However, a fair interpretation of the available data would seem to indicate a lack of strict correlation between a gonad hormone state and sexual behaviour. Care must therefore be exercised in attributing mental attitudes to hormonal states.

A few cases have been reported of the experimental induction of sexual responses in birds by the administration of gonadal hormones. In 1932, Domm and van Dyke demonstrated that male chicks from 9 to 13 days old that had received injections of hebin¹ began a few days later to exhibit the characteristic postures of adult cockerels in crowing, treading, and other sexual responses which are normally displayed by cockerels several weeks older. More recently, Allee and Collias (1938) and Allee, Collias and Lutherman (1939) have shown that hens injected with male hormone (testosterone propionate) rise in the pecking order. This treatment partially reversed the sex of the hens and the change in their behaviour was therefore to be expected, since males normally dominate females. Shoemaker (1939) obtained similar results with female canaries, and Leonard (1939) has shown that when a female canary is injected with male hormone, it will sing like a male. More extended treatment of the same nature in the Night Heron results in complete functional sex reversal. The experiments of Noble and Wurm (1938) are worth summarizing. Both sexes of the Night Heron develop during the breeding season a marked melanization of the lores, lower mandible and buccal cavity; also a vascularization of the legs which gives them a pinkish colour. These modifications may be produced in gonadectomized adults or in immatures by injections of testosterone propionate. Castration during the breeding season effects a loss of pigmentation in male and female. Oestrogens (theelin, oestrone acetate, amniotin and follutein) fail to produce any of these changes. Hence the seasonal changes in the secondary sexual characters of the Night Heron are probably due to male hormone in both sexes. Oestrogens hypertrophy the oviduct of the spayed adult or the immature, but have no effect on the vasa deferentia.

¹ An extract of the anterior pituitary which contains luteinizing hormone and follicle-stimulating hormone as well as thyrotropic hormone.

Testosterone propionate hypertrophies the latter, but also causes some enlargement of the oviduct.

Testosterone propionate will induce male sexual behaviour in adult females or in immature birds of both sexes. Even in month-old chicks it will make the voice more guttural and will induce territory defence, nest building, all male courtship ceremonies, copulation, and later brooding. Differences between the sexual behaviour of the adults seem regulated only by differences in the amounts of male hormone normally found in these birds. Oestrogens alone fail to stimulate any breeding behaviour in either sex.

All these observations point to the presence of complex endocrine mechanisms which activate, maintain temporally, and eventually displace the different types of behaviour which together constitute the reproductive cycle. The whole subject is ready for a vast amount of investigation by the experimental physiologist.

THE PERCEPTUAL FIELD OF PENGUINS

Many observations on birds and mammals show that they respond, not to simple physico-chemical stimuli, nor to isolated perceptual objects, but to perceptual complexes; to things perceived in their relationship to one another. According to the Gestalt theory, the perceptual field is essentially an organized whole, of which the parts or presumed elements are not really distinct or separate, but are characterized largely by their relations to the whole. Visual perception is not simply the physiological action of light-stimuli upon the retinal elements producing a mosaic of unrelated light-stimuli. The details of the image are unimportant. What really matters is the general pattern of the image as an organized whole. It is essentially to patterns and not to a mosaic of retinal images that the bird responds. There is justification, therefore, in treating perception as something distinct from physiological stimulation.

When a female bird responds to the posturing of a male, she does not respond directly to the physical action of the light rays reflected from him, but to her own perception of the male in relation to her own requirements.

We have very little knowledge of the perceptual field of penguins, but it is possible to discover some of the significant behaviour sequences or visual and auditory stimuli to which they make significant responses. It is important that these responses are only evoked at the appropriate times when they are the dominant need of the moment. Each bird selects from its possible perceptual environment only those features which are of functional significance to it, and ignores the rest. For example, a penguin obviously has good powers of hearing, yet while displaying or copulating it may completely ignore the loud shouts of a human being only a few yards away. Many reported cases of "short-sightedness" or "dull intellect" are probably examples of penguins confronted with situations outside their perceptual field. Their inability to recognize their normal food out of water, unless artificially conditioned to do so, is a typical example; and for this reason it is extremely difficult to devise experiments to test their powers of discrimination. Their high power of visual acuity is demonstrated when they jump out of the water on to rock or ice. Penguins invariably rise

at precisely the right moment, the exact distance presumably being "judged" during a momentary survey of the landing-place from a distance, before they dive.¹ Yet Gentoo Penguins normally show no apparent recognition when eggs are substituted for their chicks. They merely sit down to incubate instead of feeding their young; and if their eggs are placed immediately beside the nest they will continue to incubate on the empty nest for some hours.

The concept of "releasers" put forward by Lorenz (1935, 1937) marks a very important advance in our understanding of bird behaviour. Evidence continues to accumulate which shows that comparatively complicated sets of reactions may be released by a simple combination of stimuli, and that a bird responds only to a small but characteristic combination of stimuli. Such releasing stimuli must, of course, work in conjunction with internal factors which are active only at a particular season, and as Lack (1939) has suggested, there may be small variations in the internal state during the "appropriate" season. The predisposing state may be so weak that the normal releaser fails to induce the reaction, or, alternatively, so strong that the reaction is performed in the absence of the normal releaser, although usually the two are balanced.

Most of this paper has been concerned with the physiological aspects of the behaviour phases, but the whole problem also requires treatment in terms of perception. Physiological analysis of the constituent parts of behaviour has the great disadvantage that it cannot take into account the continuity of the actions as a whole. To quote R. H. Wheeler (1929, p. 77): "Any reaction of the . . . organism-as-a-whole is a uniform response made to a total situation of some kind, and if to a specific detail, always to that detail in relation to other details. We may call this total situation a stimulus-pattern or arrangement of stimuli. . . . The reaction of the organism-as-a-whole is a pattern-reaction, or configurational (i.e., Gestalt) response, and is not composed of isolated movements or a combination of discrete habits, instincts and wishes. It is an organized unit, and we call it a configurational response to emphasize the fact that it is *first*, a response to a total pattern of stimuli, and *second*, that it is not a summation of discrete responses to discrete stimuli."

Each characteristic behaviour phase appears to have little meaning unless considered in relation to its place in the cycle as a whole. There is a chain of stereotyped behaviour acts correlated with physiological processes which are all closely related to each other. Bird behaviour must surely be explained partly in physiological and partly in psychological terms, for endless difficulties arise through investigating it by either method alone.

¹ Levick (1914) records that *Pucheranphus adeliae* can leap as much as 5 feet, the "take-off" being about 4 feet from the edge, and the whole of the necessary impetus being gained as they approach beneath the water.

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APPENDIX I

THE DIVING OF PENGUINS

Except during the breeding season, most of the penguins spend their whole time at sea. They invariably swim and catch their food under water, and are supremely adapted for an aquatic life. The speed at which they can travel in the water is greater than that of most fish. From time to time rather cruel and useless experiments have been carried out to discover how long they can remain under water alive. Little accurate information is available, and I am therefore greatly indebted to Dr. P. Scholander of Universitetets Fysiologiske Institut, Oslo, who has sent me some observations on spontaneous diving periods made on captive birds. These observations refer to *Eudyptes chrysolophus*, *Aptenodytes patagonica* and *Pygoscelis papua*, and are shown graphically in fig. 2. The birds were released one at a time on a small lake, and the duration of the dives and intervening periods spent on the surface were timed continuously with a stop-watch. It will be seen that spontaneous dives rarely surpass one minute, but that in all three species the greater time is spent under water. The average diving periods seem to be rather longer than those of other diving birds, the longest being a 2-minute dive of *E. chrysolophus*. The average duration of the pause which follows each dive is nearly always less than that of the dive. In the laboratory, *E. chrysolophus* may survive a dive of 4 minutes, but 3 minutes appears to be dangerous. *P. papua* is able to survive for as long as 6 minutes.

Dr. Scholander determined the depth of dives by fastening manometres on to some of the birds. Swimming free for about 20 minutes, *E. chrysolophus* and *P. antarctica* did not dive below 5 metres. It is improbable that they normally dive to greater depths.

When travelling fast in a straight line, penguins leave the water for breath by a leap into the air at intervals which vary from 5 to 50 yards, or more. The intervals are shorter the greater the speed; a fact which is especially noticeable when they are being chased by a seal.

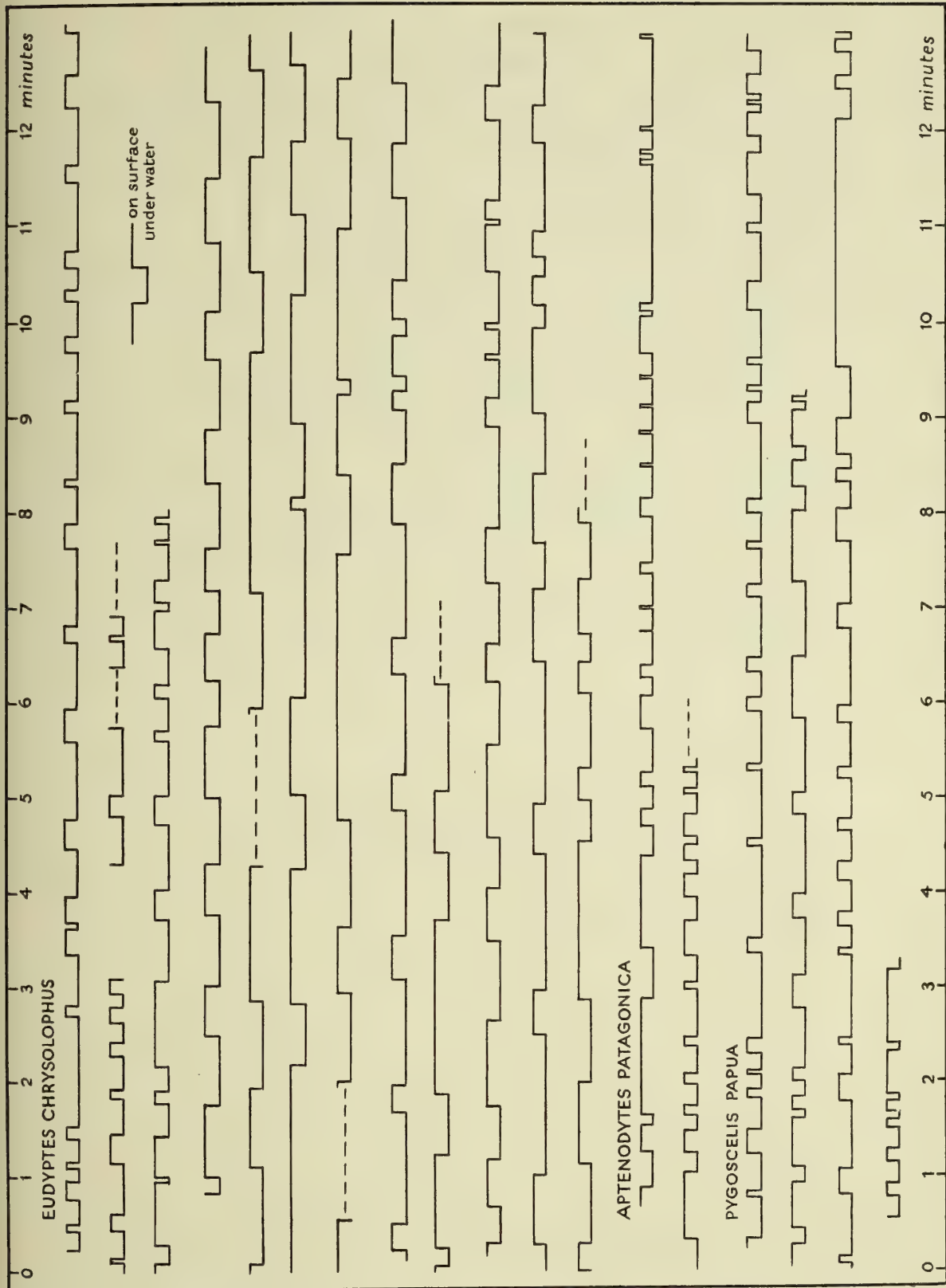


FIG. 2—Spontaneous diving periods of penguins. (See Appendix I)

APPENDIX II

SCIENTIFIC NAMES OF BIRDS MENTIONED IN THE TEXT

(See p. 199 for penguins)

- Colymbus stellatus* Pontop., Red-throated Diver.
Podiceps c. cristatus (Linn.), Great Crested Grebe.
Diomedea exulans Linn., Wandering Albatross.
Macronectes giganteus (Gmelin), Giant Petrel.
Oceanites oceanicus (Kuhl), Wilson's Petrel.
Fulmarus glacialis (Linn.), Fulmar Petrel.
Pelecanus conspicillatus Temminck, Australian Pelican.
Threskiornis aethiopicus (Latham), Black-headed Ibis.
Nycticorax nycticorax (Linn.), Black-crowned Night Heron.
Anas platyrhynchos (Linn.), Mallard.
Tadorna tadorna (Linn.), Sheld-duck.
Lyrurus tetrix britannicus Witherby & Lönnberg, Blackcock.
Bonasa umbellus (Linn.), American Ruffed Grouse.
Gallinula chloropus (Linn.), Water-hen.
Vanellus vanellus (Linn.), Lapwing.
Phalaropus lobatus Linn., Red-necked Phalarope.
Larus argentatus Pontop., Herring Gull.
Larus fuscus Linn., Lesser Black-backed Gull.
Sterna hirundo Linn., Common Tern.
Anous minutus Boie, White-capped Noddy.
Nestor notabilis Gould, Kea.
Manacus v. vitellinus (Gould), Gould's Manakin.
Melospiza melodia (Wilson), American Song Sparrow.
Erithacus rubecula melophilus Hart., Robin.
Serinus canarius (Linn.), Canary.
Sturnus vulgaris Linn., Starling.

BRIEF SUMMARY

This paper is concerned mainly with the sexual behaviour of penguins, and is based on observations made in Graham Land (Antarctica), South Georgia, and the Falkland Islands. The enquiry aims at furthering knowledge of the responses which birds make to external (exteroceptive) and internal (proprioceptive) stimulation. The known facts about the characteristic behaviour phases of the breeding season are discussed in relation to recent advances in endocrinology, and additional evidence is brought forward that a close correspondence exists between the cycle of internal changes in the mature bird and the sequence of activities which it is able to perform. The synchronization of the male and female rhythms and the stimulation of ovulation are discussed, and evidence is presented in support of the view that visual stimuli are capable of regulating many aspects of reproductive physiology and behaviour in birds.

Seventeen species of penguins are recognized, and some of their outstanding "functional characters" are described and compared. The existence of fundamentally the same behaviour patterns among the strongly differentiated, widely distributed, members of each family, and their development with structure, indicates that these are as much a part of its evolution as form.

The unique opportunities offered by penguin colonies for the study of social organization are pointed out, and some preliminary problems are discussed.



FIG. 3.—*Aptenodytes patagonica*: Ecstatic attitude while "trumpeting".



FIG. 4.—*Pygoscelis papua*: Ecstatic attitude while "crowing".



FIG. 5.—*Pygoscelis antarctica*: Ecstatic attitude while "crowing".



FIG. 6.—*Spheniscus demersus*: Ecstatic attitude while "braying".



FIGS. 7 & 8.—*Pucheranpthus adeliae*: Mutual epigamic display; swaying heads and necks alternately to right and left.



FIGS. 9 & 10.—*Pygoscelis antarctica*: Mutual epigamic display; swaying heads and necks alternately to right and left.



FIG. 11.—*Aptenodytes patagonica*: One phase of mutual epigamic display; standing for long periods with bills crossed.



FIG. 12.—*Eudyptes cristatus*: Epigamic and aposematic display; rapid side to side movements of the head. Note the crests.



FIG. 13.—*Pygoscelis papua*: Carrying grass which is laid at the feet of the bird which is being courted.



FIG. 14.—*Pucheranphus adeliae*: Carrying pebble.



FIG. 15.—*Aptenodytes patagonica*: Male urging female to lie down before copulation.



FIG. 16.—*Spheniscus magellanicus*: Epigamic display in burrow; repeated twisting of the head from side to side.



FIG. 17.—*Pygoscelis papua*: Early copulatory behaviour; reactions incomplete.



FIG. 18.—*Pucheranphus adeliae*: Normal copulation.



FIGS. 19 & 20.—*Pygoscelis papua*: Nest relief ceremony when one sex takes over incubation from the other. Illustrating also the typical bowing in epigamic display.



FIG. 21.—*Pucheranpus adeliae*: Bowing during nest relief ceremony.



FIG. 22.—*Aptenodytes patagonica*: Characteristic attitude while incubating.



FIG. 23.—*Pucheranpthus adeliae*: Fighting; one bird on nest.



FIG. 24.—*Pucheranpthus adeliae*: Aposematic display.



FIG. 25.—*Pucheranpthus adeliae*: Fighting.

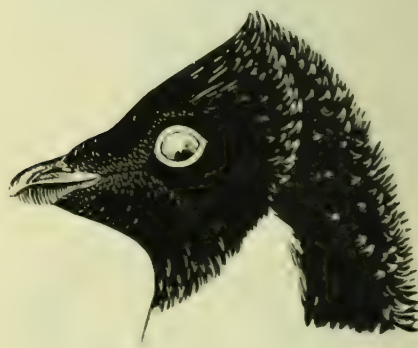


FIG. 26.—*Pucheranpthus adeliae*: Aposematic display. Note the raised crest.

DESCRIPTION OF PLATE I

Testis sections from *Pygoscelis papua*, $\times 40$

(The figures in brackets are those of the original specimens referred to in Tables I & V)

- FIG. 1 (316).—*Stage before birds congregate at their rookeries.* Many spermatocytes dividing but more mature stages absent. Tubules occluded in most cases.
- FIG. 2 (333).—*Early courtship activities at rookery.* All stages to sperms with wavy tails, mostly held in clumps. Well defined lumen in nearly all tubules with small number of free spermatozoa.
- FIG. 3 (338).—*Nest building.* All stages present. A few free spermatozoa, but most are held in groups round the tubule. Some tubules without a lumen, yet containing all stages; others having small number of loose degenerating cells in the lumen.
- FIG. 4 (337).—*Same date as fig. 29. Made incompleated attempt to copulate.* Slightly more advanced than fig. 29. Great nuclear activity in spermatocytes and many more spermatids than in fig. 29, but about the same number of free spermatozoa. Some tubules without any lumen.

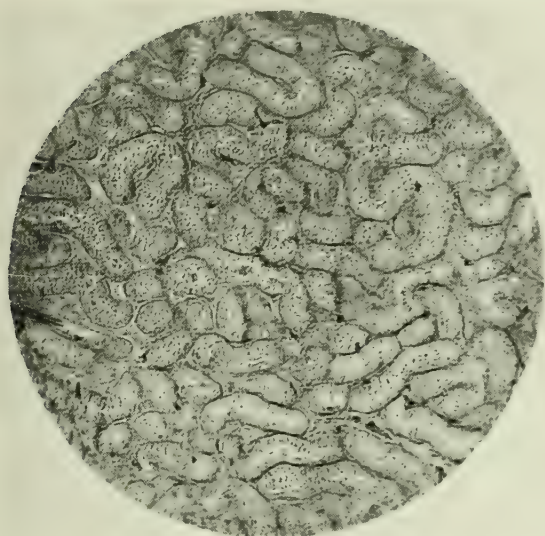


Fig. 1

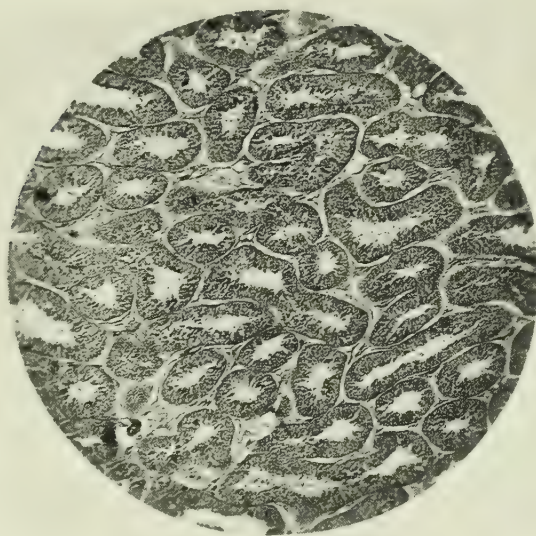


Fig. 2

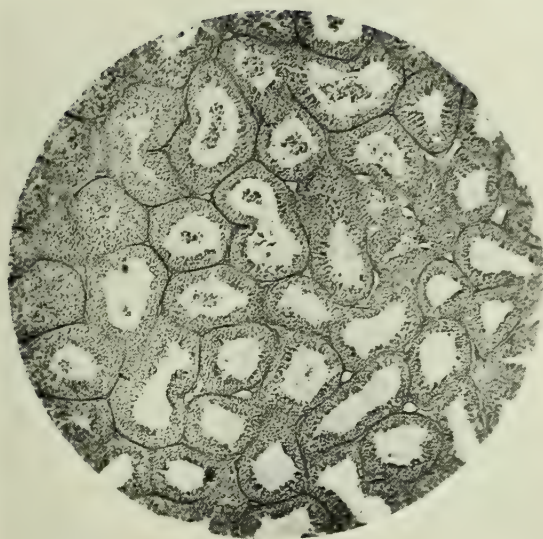


Fig. 3

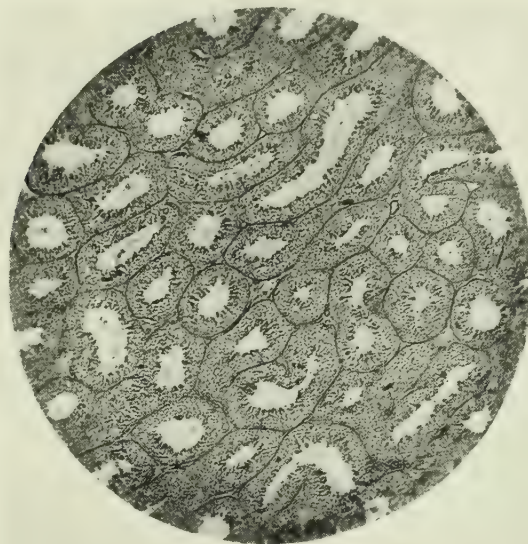


Fig. 4

DESCRIPTION OF PLATE II

Testis sections from *Pygoscelis papua*, $\times 40$

(The figures in brackets are those of the original specimens referred to in Tables I & V)

- FIG. 1 (350).—*Watched copulating*. All stages present with many more spermatozoa free in the lumen of most tubules.
- FIG. 2 (518).—*Feeding newly-hatched chicks*. Most cells round the periphery of the tubules are in a state of rest. A few spermatogonia show some activity. Lumen present in most tubules with sloughed off degenerate cells in centre. No spermatids or later stages.
- FIG. 3 (577).—*With chicks in second down*. A few spermatogonia show some activity. Very few spermatocytes. Lumen present in most tubules with sloughed off degenerate cells in centre.
- FIG. 4 (282A).—*Just completed moult*. Advanced retrogression, but some signs of activity in a few spermatogonia. Very few spermatocytes. Tubules mainly full of debris.

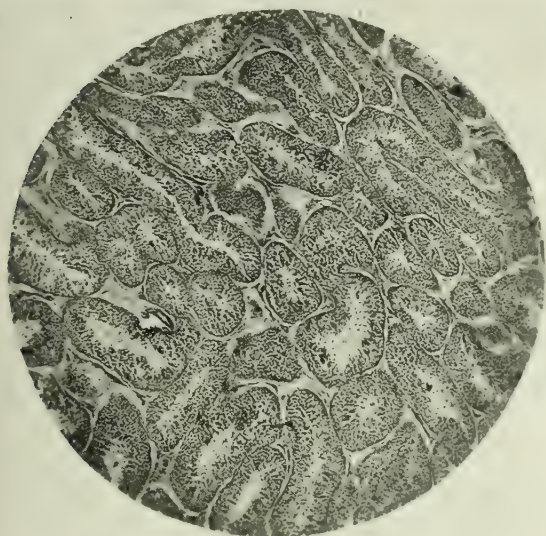


Fig. 1



Fig. 2

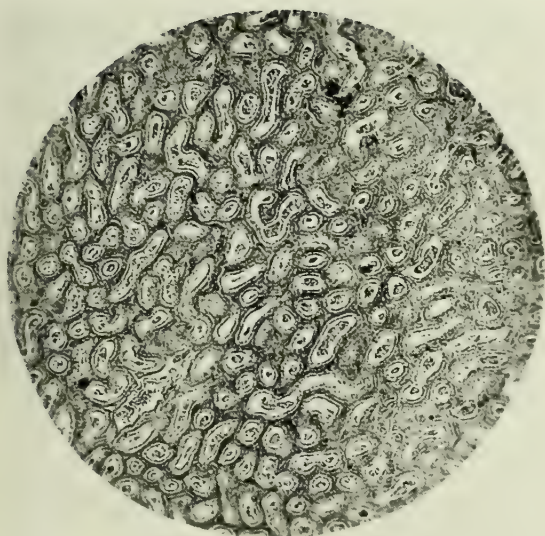


Fig. 3

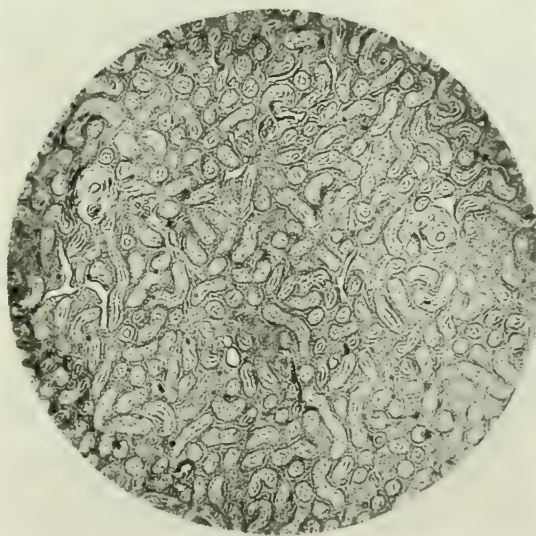


Fig. 4



FIG. 1.—*Pygoscelis papua* at nest, South Georgia.



FIG. 2.—Colony of *Pygoscelis papua*, Bay of Islands, South Georgia.



Aptenodytes patagonica. Chicks about 10 months old in "crèche" (see p. 224), Bay of Islands, South Georgia.

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*ON TWO NEW SPECIES OF THE
HYDROID MYRIOTHELA*

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and the British Museum (Natural History)*

WITH FOUR PLATES AND NINE TEXT FIGURES

LONDON

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MYRIOTHELA PENOLA sp. nov.

ORIGIN OF THE MATERIAL

Two specimens of *Myriothela penola* were found by the British Graham Land Expedition 1934-37 floating alongside R.Y. *Penola* in a creek at the Argentine Islands. Ice was floating on the surface of the water, which was about 2 fathoms in depth. Both specimens were attached to the apex of a pennatulid, a species of *Virgularia*, which had been torn from its substratum. The soft tissue of the pennatulid was absent from the upper 10 cm. of the animal, and the hydroids were attached directly to the horny axis. One apparently mature female individual measures 850 mm. in length and bears actinula larvae ready for liberation. The smaller male specimen is about 55 mm. long and bears very young blastostyles and rudimentary gonophores. The specimens were preserved in formalin after narcotization with tobacco.

GENERAL DESCRIPTION OF THE HYDROID (pl. I, fig. 10)

Tentacles are restricted to the distal $\frac{5}{6}$ of the hydranth. This region is tapering in shape, about 75 cm. long with a diameter at the oral end of 7.5 mm. increasing to 30 mm. proximally. The aboral $\frac{1}{6}$ of the hydranth, about 10 cm. in length and 12 mm. in diameter, is devoid of body tentacles, and bears numerous lobed blastostyles carrying tentacles on the lobes. The hydrorhiza is in the form of adhesive tentacles which spring from the base of the hydranth and from some of the proximal blastostyles. There is no perisarc, but the adhesive tentacles, when attached, are capped by a chitinoid disk. The species is dioecious, an immature male and a mature female are known. The colour of the living animal closely resembles that of *M. austro-georgiae* (Jäderholm, 1905, pl. 1), the tentacle bearing zone being bright orange, the gonophores white, and the blastostyles ranging from orange to light greenish-brown. A coloured sketch was made of the living animal which has enabled a direct comparison to be made with the coloured plate of *M. austro-georgiae*.

NEMATOCYSTS

No nematocysts have been seen in the discharged state, but four types can be seen in sections (fig. 1). Similar preparations have been made of *M. cocksi*, because the nematocysts of this species have been described by Weill (1934). In *M. penola* mature haplonemes have been found only on the younger and larger body tentacles, and on the tentacles of small young blastostyles, but the other three types occur on the body wall and on older tentacles of both hydranth and blastostyles. Details of the distribution of the nematocysts are given with the description of the various parts.

Desmonemes are of variable size. The capsule measures 9-18 μ , and contains a thick thread coiled into about $2\frac{1}{2}$ turns. The thread stains red and the capsule contents remain unstained with Mallory's triple stain. The lasso thread is conspicuous and the cnidopod is very stout and anchored by numerous rooting threads to the fibrils of mesogloea in the capitulum of the tentacle. These roots do not appear to penetrate into the mesogloea, but end as darkly staining thickenings on the ends of

Heteroneme Stenotele Desmoneme Haploneme Heteroneme Stenotele Desmoneme Haploneme

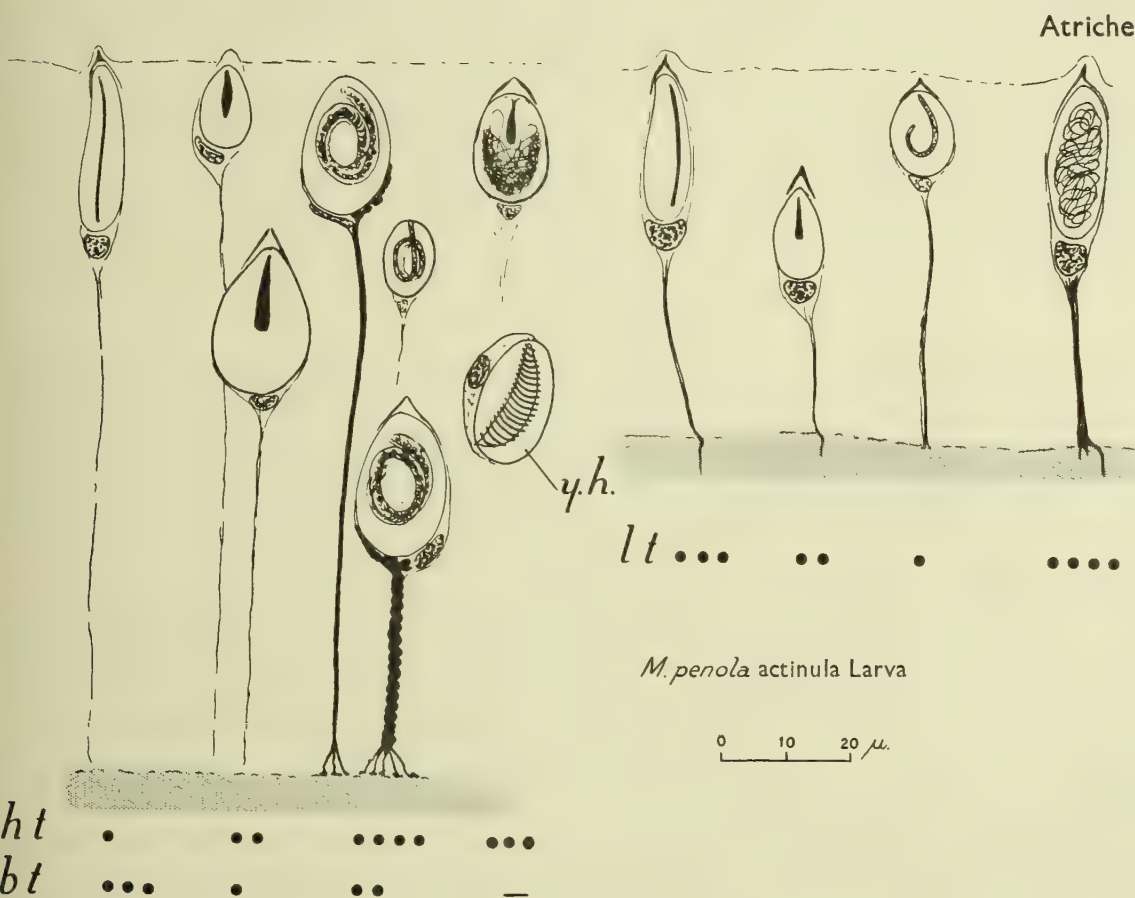
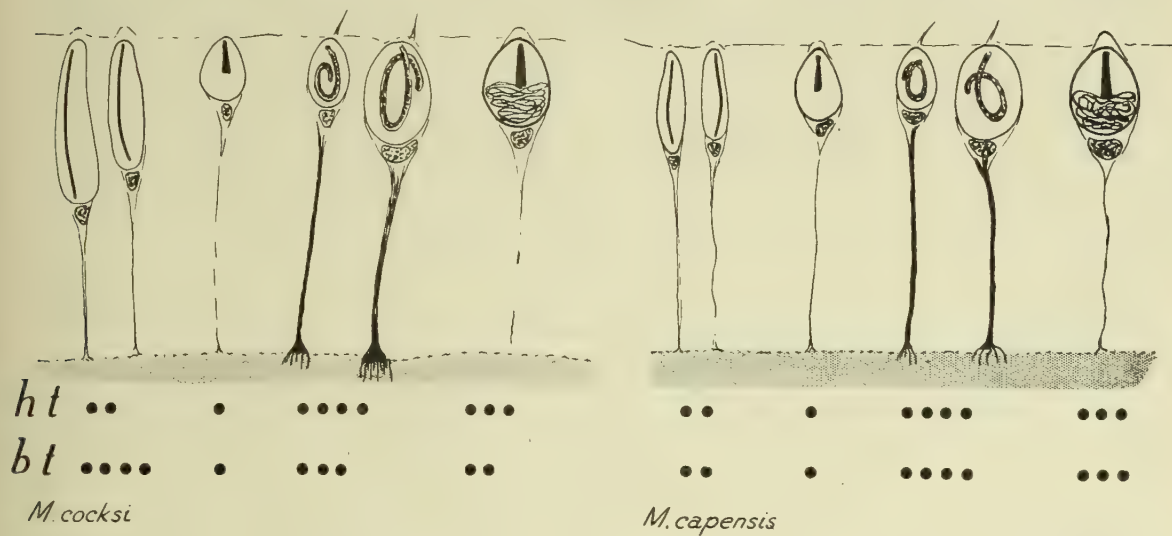


FIG. 1.—Diagrams illustrating the composition of the endome of *M. cocksi*, *M. capensis*, and *M. penola*. The relative abundance of the different types of nematocyst on the body tentacles "h.t.", on the blastostyle tentacles "b.t.", and on the long provisional tentacles of the actinula is shown by the number of black dots below each type. The mechanical tint represents the mesogloea.

the fibrils (pl. III, fig. 22). When a desmoneme is situated deeply in the ectoderm the cnidopod fibre appears to be tightly twisted in a spiral, but as the capsule approaches the surface of the epithelium the cnidopod elongates and its coils become straightened (pl. III, figs. 22 and 23). These cnidopods are much stouter than those of other types of nematocyst in *M. penola*.

Haplonemes are almost uniform in size, the ovoid capsule measuring $13 \times 9 \mu$. The capsule contents stain little with Mallory's triple stain, and the thread forms a refringent yellowish basal mass of predominantly transverse coils. The developing haplonemes from the tentacle nurseries show the thread coiled in about 20 regular transverse turns (fig. 1, "y.h.").

Heteronemes are of two types, both showing blue-grey capsule contents and a red axial body after Mallory's triple stain. Those with an elongated pyriform capsule are fairly uniform in size, attaining $20 \times 5-6 \mu$, and they show a slender axial body of almost even thickness. Ovoid *stenoteles* are variable in size, the capsule measuring 10×7 to $18 \times 13 \mu$. The axial thread can only be seen in the upper half of the capsule and increases in thickness towards the middle of the capsule.

The capitula of the transitory larval tentacles of the actinula are mainly armed with a type of nematocyst unlike those of the adult. This presumably is comparable with the atriche of the actinula of *M. cocksi*. The capsule is ellipsoid (or possibly ovoid), $18 \times 7 \mu$, and contains a fine thread staining purplish with Mallory's triple stain, the capsule contents remaining unstained. The cnidopod is well developed, appearing brilliantly red with the above stain, and shows one main rooting process sunk into the outer part of the mesogloea (pl. IV, fig. 29).

BODY WALL

The body wall is about 200μ in thickness at the oral end and increases to 400μ in the proximal part of the tentacle bearing zone (it has not been sectioned in the blastostyle zone). The *ectodermal* epithelial cells are much elongated and are covered by a thin cuticle (pl. III, fig. 25, "cu."). The superficial cytoplasm of these cells contains a variable number of fine granules which may form a dense superficial layer; they stain black with iron haematoxylin and red with Mallory's triple stain. These granules are present everywhere, but are more numerous on the tentacles, blastostyles, and hydrorhiza (fig. 6 and pl. II, fig. 19) and most abundant on degenerating tentacles (see p. 261 and p. 264). Nematocysts lie at various depths in the ectoderm outside the muscle and mesogloea layer, desmonemes being the most frequent type. The mesogloea forms a solid cylindrical sheet, its thickness of $45-90 \mu$ being greatest towards the aboral end. Longitudinal ridges of mesogloea project from this sheet into the ectoderm and bear the longitudinal muscle fibres over their surfaces. All other ectodermal elements are excluded from the furrows between the ridges. Towards the oral end where the musculature is more compact, the ridges project for $25-35 \mu$ and are set at intervals of $10-15 \mu$ or less (pl. III, fig. 28), while at the aboral end of the tentacle zone the ridges are 120μ deep and set at intervals of about 30μ .

The *endodermal* epithelium forms a regular peripheral layer of columnar cells with their circular muscle processes lying against the smooth inner surface of the cylinder of mesogloea. Most of these cells are binucleate with scanty, lightly staining

cytoplasm; many are probably ciliated. Gland cells are irregularly distributed. At intervals of about 0.3–0.5 mm. endodermal villi project into the enteron forming longitudinal ridges 1.5 mm. deep (fig. 2). They are mainly parallel, and 80–150 may be seen in one transverse section. The free edges of adjacent villi occasionally unite (this is probably caused by their manner of growth, see p. 262). A flange of mesogloea 7μ or less in thickness projects into each villus separating the two layers of endoderm. The peripheral $\frac{1}{2}$ – $\frac{3}{4}$ of each villus is composed mainly of cubical vacuolate cells, each possessing two similar nuclei, very little cytoplasm, and sometimes a few nutritive spheres. Gland cells lie among the vacuolate cells in the upper part of the hydranth. The free inner $\frac{1}{4}$ or $\frac{1}{3}$ of each villus is composed of darkly staining cells which are mostly binucleate and contain coarse granules of various sizes. These cells probably represent the apical cells restricted to the extreme edge of the villus in other species, and they probably carry out intracellular digestion. In some parts the darkly staining edges of the villi are in a disintegrating condition. This may be an artefact, or it may indicate that disintegration and casting off of parts of the villi occur in *M. penola* as in *M. cocksi* (Allman, 1875). I have not been able to find such a condition in the available specimens of *M. cocksi*; and the process described by Allman may thus be intermittent in occurrence. A more detailed description of the histology of the endoderm of the hydranth body is not possible owing to damage caused by the folding and bending of such a large animal since it was preserved. There is no reason to believe that cell elements described for other species and not mentioned above are in reality absent from *M. penola*. The enteron of the main body of the hydranth is continued into the blastostyles and into the hydrorhiza tentacles.

BODY TENTACLES

About 330,000 tentacles cover the distal 75 cm. of the hydranth. The tentacles are 0.5–2.5 mm. in length, becoming smaller towards the proximal part of the body. The tentacles on the oral few centimetres are largest and most elaborate in structure, and the smaller tentacles, except for those round the mouth (see p. 262), show progressive stages of degeneration. The fully formed tentacle bears a rounded capitulum 0.6 mm. in diameter, the stem being 0.4 mm. or less across and sharply demarcated from the capitulum. The structure of the tentacle is more elaborate than in any hitherto described species of *Myriothela*, and is shown diagrammatically in fig. 2. The mesogloea is represented by heavy black lines, and the external longitudinal and internal circular muscles have been omitted from the figure. In the capitulum the mesogloea is produced externally into a pad of radial fibres up to 180μ in length. This is covered by an ectodermal layer of 60μ with the cell nuclei lying at various levels. Nematocysts are close together through the whole ectodermal thickness, and they do not form mainly a peripheral layer as in some species. Desmonemes with very stout anchoring cnidopods (see p. 256) are most numerous. In large young tentacles haplonemes are next in abundance and occur all over the capitulum, but in ageing tentacles situated only a few centimetres behind the mouth and post-orally no mature haplonemes are found. Stenoteles are always present and various in size, and they become more numerous as the haplonemes disappear in older tentacles. Heteronemes of uniform dimensions are always present but are the least abundant

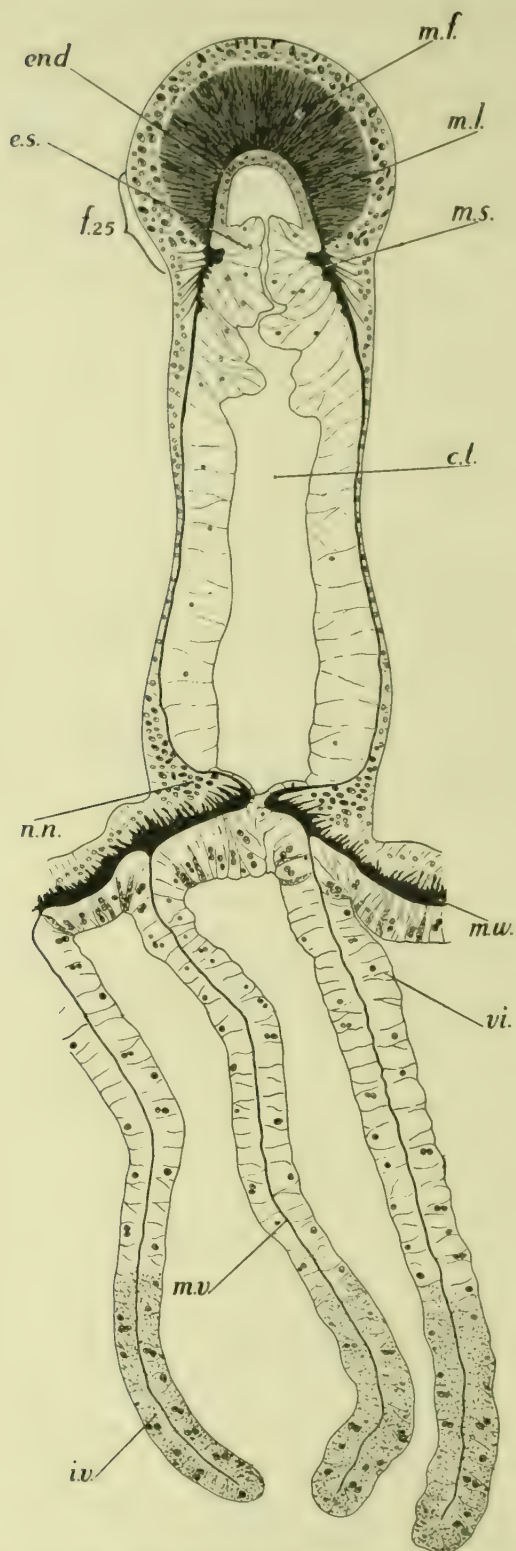


FIG. 2.—*M. penola*. Diagrammatic transverse section of hydranth body, from about 15 cm. behind the mouth, showing a tentacle in sagittal section and the endodermal villi. The mesogloea is shown by heavy black lines and the musculature is omitted. $\times 77$.

type. The endoderm forms a regular layer of darkly staining small columnar cells lining the capitulum.

At the junction of the capitulum and stem a sphincter of elongated endodermal cells leaves a narrow channel connecting the cavity of the capitulum with that of the stem. These cells resemble those of the stem in staining reactions. This sphincter is supported by a thick ring of mesogloea bearing internal circular ridges which are covered by well-developed circular muscle fibrils (text-fig. 2 and pl. III, fig. 25 "c.m.") Externally this ring of mesogloea sends processes out into the ectoderm.

The stem of the tentacle is covered by a thin ectodermal epithelium of 6–15 μ which is almost devoid of nematocysts, and is lined by lightly staining cubical or columnar endodermal cells which are extensively vacuolated and which surround a wide cavity. The endoderm is continuous with that of the body through a narrow basal perforation of the mesogloea (fig. 2). Whether a narrow channel putting the lumen of the tentacle into communication with the general enteron exists could not be determined with certainty; most sections do not show any clear channel through this endoderm although the mesogloea is perforated. Where the mesogloea of the tentacle converges towards the body wall mesogloea around the perforation, the ectoderm is thickened and is richly provided with developing nematocysts, appearing to form a nursery from which nematocysts migrate. The most abundant type in the nursery is a developing haploneme (fig. 1 "y.h."). I am indebted to Dr. Weill for its identification. Stenoteles are next in frequency followed by heteronemes. Young desmonemes are frequent, but fully formed ones are rare.

The smaller tentacles covering the middle and lower part of the tentacle zone are undoubtedly older and in process of dedifferentiation and absorption. The majority are 1–0.5 mm. in height, but those at the proximal edge of this zone are smaller still. The structure of the tentacles becomes simpler with decrease in size, the nematocysts become fewer, and the nursery may appear almost worked out. The endodermal valve below the capitulum and the supporting rim of mesogloea disappear. In longitudinal section such a tentacle resembles those of smaller species such as *M. capensis* (fig. 7, b). The capitulum then shrinks and merges into the stem and the pad of radial mesogloea fibres becomes shorter, the height of the pad being 18 μ in a tentacle 0.45 mm. in length. The stem shortens and its ectoderm thickens and becomes indistinguishable from that of the capitulum. The superficial granules in the ectodermal cells (see p. 258) become increasingly abundant as the tentacle shrinks.

In the fully formed tentacles near the mouth, which are those most essential for feeding, the presence of the supported muscular sphincter at the base of the capitulum must make possible the closure of the endodermal canal. This will enable the turgidity of the capitulum to be maintained during movements of the tentacle. Serpentine body movements of a feeding *Myriothela* have been described by Billiard (1921), and if there is an opening at the base of the tentacle, pressure changes of the enteric fluid may be transmitted to the tentacle, but need not pass the capitular sphincter.

GROWTH OF THE BODY

That growth in length of the hydranth body takes place most actively at the extreme oral end is indicated by the structure of the body wall, and by the position

of the young tentacles. The endodermal villi become less deep and disappear just within the edge of the mouth. Immediately behind the oral union of ectoderm with endoderm a thin layer of material can be seen between the two epithelia, but it stains in the same manner as does the cytoplasm of the cells. Post-orally this layer thickens and gradually takes on the blue colour with Mallory's triple stain which is typical of mesogloea, and when considerable thickness is attained the external lamellae begin to appear and become larger with increasing distance from the mouth. Such a series of developmental stages of the massive mesogloea layer would be expected to be found in this position if linear growth takes place actively at the oral end. On the ectodermal side of the mouth rim can be found a few small tentacles which are undoubtedly young. They are rich in nematocysts and their capitula are quite distinct from the stem, although both may be half the size of these parts in a fully formed tentacle, and their apical mesogloea fibrils are well developed. Tentacles reduced in size by degeneration do not show these features (see p. 259), and the small tentacles below the oral 6 cm. show progressive stages of degeneration. Thus new tentacles arise at the oral end, but others must also grow between existing tentacles as the body increases in diameter.

If the tentacle bearing zone increases in length mainly by a circumoral growth zone, its growth in diameter must take place gradually throughout much of its length as the greatest diameter is found in the older lower part of the tentacle bearing zone. The union of the free ends of some of the endodermal villi is indicative of increase in diameter after the original villi have been formed. This can be seen in the developing spadices of the gonophores where increase in size leads to sub-division of some of the original villi, a peripheral division of the villus taking place progressively from without inwards as the diameter of the spadix increases.

At the proximal end of the tentacle bearing zone the dedifferentiating tentacles become completely absorbed. The body wall contracts in diameter and young blastostyles make their appearance (pl. I, fig. 10, "z. y. b."). The blastostyles increase in size post-orally. Full sized blastostyles are absent from the oral 2 cm. of the blastostyle bearing zone (fig. 10) although they are present elsewhere. In both specimens some of the small blastostyles are appearing before the tentacles are completely absorbed at the junction of the tentacle and blastostyle bearing zones. Thus it may be concluded that the blastostyle bearing zone increases in length at its oral end at the expense of the tentacle bearing zone.

BLASTOSTYLES

The proximal $\frac{1}{6}$ of the larger hydranth bears about 300 mature blastostyles 20–25 mm. in length, and a smaller number of shorter immature blastostyles situated at the distal end of this region and in between the larger blastostyles (pl. I, figs. 10 and 11, text-fig. 5, *a* and *d*, and pl. II, fig. 15). Mature blastostyles are irregularly lobed or branched in their middle and distal parts; this branching is absent from young blastostyles and from those of the smaller specimen (fig. 5, *d*). Short tentacles are borne on the blastostyle lobes, and where these are absent the tentacles occur on the main axis. A description of the structure of a mature blastostyle and of the structure, development, and degeneration of the blastostyle tentacles from the larger specimen follows.

The small blastostyles of the smaller specimen are simpler both externally and internally.

The *wall* of the blastostyle (pl. III, fig. 26) is a little thinner than that of the main hydranth, and resembles the latter with certain modifications.

The wall is about $180\ \mu$ thick. The ectoderm forms a regular epithelium with nuclei situated midway between the surface and the mesogloea. The superficial granules (see p. 258) below the cuticle are few at the base of the blastostyle and become progressively more numerous towards the apex. Nematocysts are absent except on the lobes bearing developing tentacles; here a nematocyst nursery may be found close to the growing tentacles.

The mesogloea is much less robust, the solid lamella being only $8\text{--}10\ \mu$ thick and the outer longitudinal ridges $9\text{--}18\ \mu$ in depth. These ridges are absent from the tentacle-bearing lobes and from tracts on the main blastostyle leading to the lobes. In the zones where the ridges are disappearing they become fewer, but often deeper, projecting farther into the ectoderm.

The endodermal cavity is continuous with that of the main hydranth. The endodermal villi, about 1 mm. or less in depth, are more frequent than in the hydranth body and their supporting mesogloea is less thick. The villi are separated peripherally by acute grooves lined with ciliated cells which also spread over the faces of the villi to a distance of $40\text{--}80\ \mu$ (pl. III, fig. 26, "f."). Gland cells are numerous at the base of the grooves lying between the ciliated cells. Many of these grooves pass directly into the lumen of the spadix of the gonophores. The free parts of the villi are composed almost entirely of vacuolate cells, gland cells are few, and the apical cell zone is almost or entirely absent (pl. III, fig. 26). A few nematocysts are sometimes present near the apical cells where these occur. The vacuolate cells each possess two similar spherical nuclei; they may contain no nutritive spheres, as in fig. 26, "vc.", but near developing gonophores or tentacles nutritive spheres are frequent.

The villi show various physiological and morphological states in different parts of the blastostyle. In the growing lobes carrying developing tentacles the vacuolate cells are young. Their nuclei are the same as elsewhere, but the cells are smaller with dense cytoplasm and a turgid appearance, the free margin being often strongly convex. Nutritive spheres may or may not be present, and stages in the formation of the vacuolate condition can be seen (pl. II, fig. 16 "e.y."). The tongue-like villi of the growing spadices also show a juvenile condition (see p. 267 and fig. 4, "vi."), and the vacuolate cells here carry more nutritive spheres than in any other region. Mature villi from the middle region of the blastostyle have been described above, but distal to the gonophores the villi are senile. No food reserves are present here and the vacuolate cells have lost almost all their cytoplasm. The gland cells are shrunken or absent, and the ciliated cells in the grooves between the villi have almost or entirely disappeared.

The *tentacles* of the blastostyle, unlike those of the hydranth body, are not clearly divisible into capitulum and stem (pl. II, fig. 17, "j."), and their bases are demarcated from the blastostyle by a constriction (pl. II, fig. 15, "t.2" and fig. 17). Fully formed tentacles are present only in the middle part of the blastostyle (fig. 5, *a*, "m.b.t."; pl. II, fig. 15, "t.2"). The apex of such a tentacle is rounded and composed of regular columnar ectodermal cells covering a pad of mesogloea fibrils about $25\ \mu$ in length

(pl. II, fig. 17). Nematocysts occur only at the apex of the tentacle where they form a peripheral layer of radially arranged and closely packed heteronemes and occasional stenoteles. In the deeper parts of the ectoderm a few heteronemes and stenoteles can be found, but they are orientated in no particular manner. Larger desmonemes, strongly anchored to the mesogloea (see p. 256), are most numerous in the deeper parts of the ectoderm. The convolutions of their cnidopods become drawn out as the capsules approach the surface (pl. III, figs. 22 and 23). Haplonemes have only been found in tentacles on small young blastostyles. Proximally the tentacle increases in diameter, and the stem mesogloea forms a simple lamella. The endodermal lumen does not communicate with that of the blastostyle, a layer of mesogloea, covered on both sides by endoderm, spanning the tentacle base. The tentacular endoderm lacks gland cells, ciliated cells, and nutritive spheres. Basally and distally this epithelium is cubical and laterally it is thicker and columnar. The apical endoderm lacks inclusions, but elsewhere fine granules staining red with fuchsin lie in the distal parts of the cells.

The *development of a tentacle* starts in the endoderm of the blastostyle. A diverticulum grows into the overlying ectoderm and becomes nipped off by the mesogloea. A hollow endodermal vesicle thus lies in the ectoderm with its covering mesogloea continuous with that of the blastostyle wall. The endodermal vesicle increases in size and elevates the overlying ectoderm. At the same time the blastostyle wall here bulges outwards so that the developing tentacle becomes borne on a lobe from the main axis of the blastostyle. The endodermal vesicle continues to increase in size, and the apical mesogloea fibrils start to develop; the overlying ectoderm thickens and the peripheral layer of nematocysts make their appearance (pl. II, fig. 16). Growth continues; the superficial ectodermal granules (see p. 258) become more abundant, and the endodermal epithelium becomes differentiated into apical, basal, and lateral parts. The full development of the mesogloea fibrils and of the nematocysts results in the mature tentacle already described (pl. II, fig. 17).

Degeneration of the tentacle follows. The lateral endoderm thickens and the elongated cells become charged with fuchsin-staining granules. The mesogloea fibrils gradually shorten (pl. II, fig. 18) till they vanish (fig. 19), the nematocysts disappear, and the apical endoderm becomes indistinguishable from that of the lateral region, the cells of both becoming distended with granules. The base of the tentacle spreads out, and the basal endoderm, also filled with granules, becomes stretched (fig. 19). Finally the shape of the tentacle becomes irregular and the apex invaginates or breaks down (fig. 5, *a*, and pl. I, fig. 14, "s.b.t." and pl. II, fig. 15, "t.3"). The ectodermal granules become increasingly abundant, but unlike those of the endoderm, they remain in a surface layer (fig. 19).

Mature *gonophores* of the female only have been seen, the gonophores of the small male specimen being immature. Not more than about 10 gonophores lie on each mature female blastostyle, and a smaller number, sometimes as many as 7, lie on some of the male blastostyles, many of which lack gonophores. The gonophores of each blastostyle form a graded series of developmental stages, all of which are different. The older gonophores are situated distal to the younger ones which may be scarcely visible externally (fig. 5, *d* and pl. II, fig. 15 "g.2"–"g.10"). Usually one gonophore only approaches maturity at a time on each blastostyle; one blastostyle of the larger specimen appears to be exceptional in bearing two advanced gonophores.

The female specimen carries 19 mature gonophores, they are about 7.2 mm. in diameter and contain an actinula larva almost ready for liberation (pl. I, figs. 10 and 11, pl. II, fig. 15 "g.10"). In two of these gonophores the wall has split and the actinula is almost free (pl. I, fig. 11 "a.e." and fig. 5, *a*). Many other blastostyles lacking an old gonophore show a shrunk knob or scar which represents the remains of a gonophore which has recently liberated its larva. The largest gonophores, apart from the above, are uniform in size and do not exceed 2.6 mm. in diameter. They are numerous, but not more than one is present on each blastostyle (pl. I, fig. 11, and pl. II, fig. 15, "g.9." In these gonophores the definitive ovum is very small, about $110 \times 80 \times 80 \mu$. The specimen must have been collected during the period of distribution of its larvae and the gonophores of 2.6 mm. diameter would have become mature in the following breeding season.

The older gonophores of the immature male specimen are of about the same size and do not exceed 0.6 mm. in diameter. These gonophores are clearly young. Their spermatocytes are equal in size and lie about 12 cells deep over the spadix, and these gonophores correspond to a stage of development intermediate between those of gonophores "g.5" and "g.6" of the female specimen (pl. II, fig. 15).

The mature female gonophore is cryptomedusoid in structure with no trace of canal system. A velar opening must be formed at a stage intermediate between the two larger types of gonophore mentioned above (pl. II, fig. 15 "g.9" and "g.10"), but such a stage is absent from the specimens. The gonophores are sessile and attached by a base 0.9 and 1.9 mm. in diameter respectively in gonophores of these two sizes. The structure of the gonophore is shown in fig. 4 and in pl. II, figs. 20 and 21, and will be described more fully with the account of the development of the gonophores given below.

DEVELOPMENT OF THE GONOPHORES

A single blastostyle from the large female specimen is shown in pl. II, fig. 15. This blastostyle has been sectioned and the development of its gonophores followed. The 10 gonophores are numbered in order of age. The youngest, "g.1" lies near the junction of the blastostyle with the hydranth, and gonophores "g.1", "g.3", and "g.6" are situated on the side of the blastostyle not visible in fig. 15. A gonophore-bearing blastostyle from the immature male specimen has also been sectioned.

In the *female* the earliest stage sectioned, "g.1" fig. 3, *a*, shows the rudiments of the spadix and bell endoderm ("r.") and of the subumbrella and spadix ectoderm ("r.e."). The former is a closed vesicle with a small lumen completely cut off from the enteric cavity. It lies mainly in the ectoderm, the mesogloea being elevated by it. The cells composing this rudiment are much smaller than those of the main blastostyle endoderm and their cytoplasm is dense and darkly staining. The rudiment is raised peripherally into a rim. The subumbrella ectodermal rudiment or "nodule médusaire" of Benoit (1925), is a rounded mass of cells which lies above the endodermal rudiment and sinks down into the hollow within the rim of the latter. The overlying ectoderm is thickened, and projects slightly above the general level. A younger stage showing the origin of these two rudiments is not present on this blastostyle, but it is probable that the ectodermal rudiment may arise from the endodermal rudiment in *M. penola*

just as Benoit (1925) described for *M. cocksi*. In three of the younger gonophores the central part of the mesogloea separating the two rudiments is very thin and appears to be interrupted in the middle. Here the cells of the two rudiments seem to be confluent, and the cytology of the cells in the two rudiments is identical at this point, thus suggesting that the mesogloea has not yet completely united after the "nodule médusaire" has passed through it from the endoderm.

With increase in size of both rudiments the endodermal rim, which will give rise to the bell endoderm, grows up and gradually encloses the subumbrella ectoderm (figs. 3, *b* and *c*). This is completed by the fusion of the mesogloea-tipped edges of

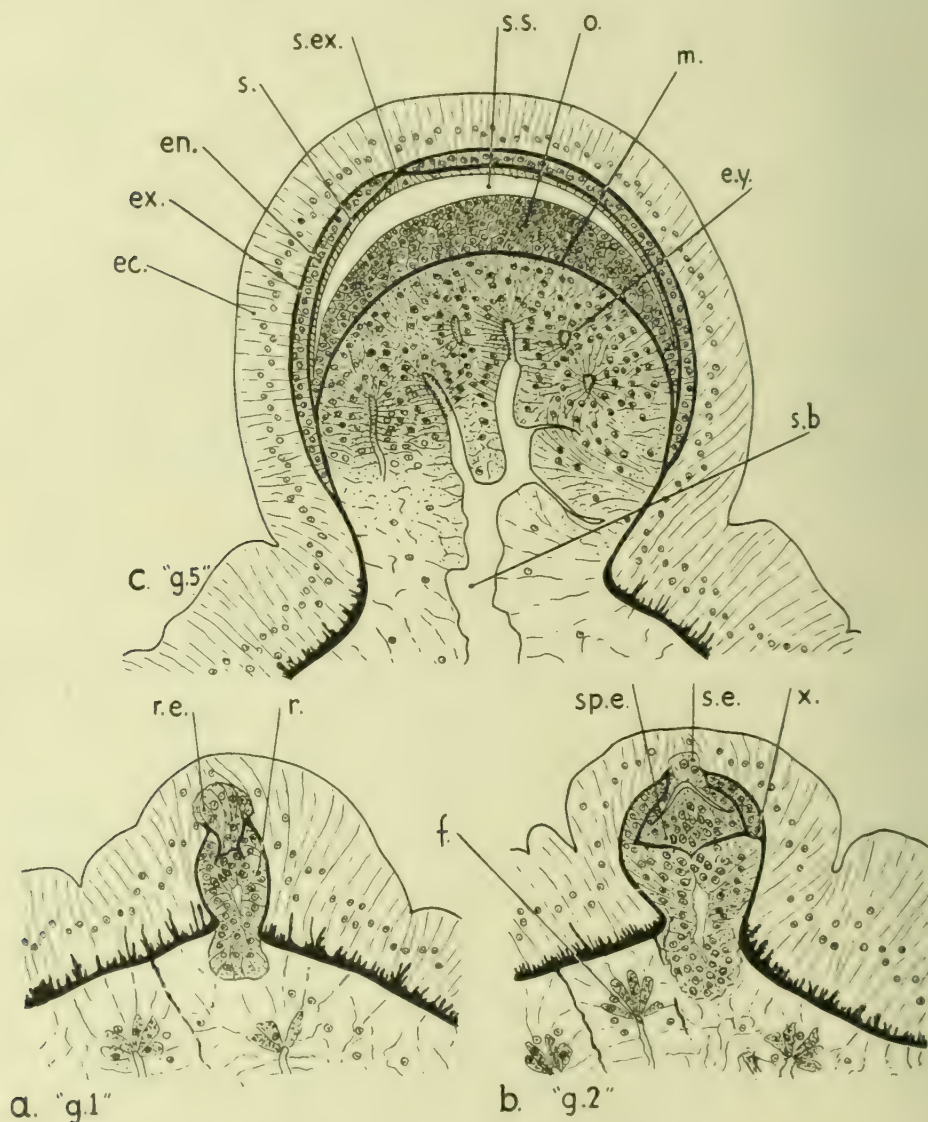


FIG. 3.—Diagrams representing sagittal sections of three stages in the development of the female gonophore of *M. penola*, from gonophores shown on the blastostyle in pl. II, fig. 15. Fig. 3, *a*, represents "g.1" which is situated on the invisible side of the blastostyle in fig. 15, fig. 3, *b*, represents gonophore "g.2", and fig. 3, *c*, represents gonophore "g.5". The mesogloea is shown by heavy black lines and the musculature is omitted. $\times 145$.

the rim. This point of fusion (fig. 3, *c*, "s.ex."), where solid mesogloea excludes the endodermal layer, persists in later stages. The mesogloea lining the rim of endoderm grows outwards at the basal angle of the rim and fuses with the outer layer of mesogloea, so cutting off the endoderm of the bell from the main endodermal vesicle. This fusion is complete on the right side only in fig. 3, *b*, "x").

The ectodermal rudiment becomes bilaminar as it increases in size. A thick layer covers the flat outer surface of the endodermal vesicle and gives rise to the germinal epithelium over the spadix; a thin outer layer becomes applied to the endodermal rim and will form the subumbrella ectoderm, the central space being the subumbrella cavity (figs. 3, *b* and *c*, "s.s."). The subumbrella ectoderm becomes very thin except below the point of fusion of the bell mesogloea (fig. 3, *c*, "s.ex."). The over-lying ectoderm forms the exumbrella covering, and thus all layers of the bell wall are laid down.

The main endodermal vesicle remains closed until the gonophore rudiment is larger than in fig. 3, *b*. As the vesicle grows its cavity elongates towards the axis of the blastostyle, and a hollow outgrowth in this direction finally puts this cavity into communication with the enteric space of the blastostyle at a stage intermediate between those shown in figs. 3, *b* and *c*. With further increase in size the endodermal vesicle bulges outwards to form the spadix (fig. 3, *c*), and its epithelium becomes furrowed so that tongue-like villi project into the central space. With further growth in diameter new villi are formed and fresh peripheral furrows are made, so that villi originally single sometimes becomes subdivided at their bases. The endodermal cells in young stages (figs. 3, *b* and *c*), and in the peripheral region against the mesogloea in older stages are small, uninucleate, and densely staining, and early become ciliated. Where the epithelium becomes continuous with that of the blastostyle the cells enlarge and lose their cilia and much of their cytoplasm (fig. 3, *c*, and pl. II, fig. 20). The villi are rounded in cross-section and lack muscles. They are entirely composed of vacuolate cells loosely attached to a core of mesogloea (fig. 4 and pl. II, fig. 20). These cells become larger, nutritive spheres appear in their cytoplasm, and some of them develop large vacuoles as they increase in age and become further removed from the growing peripheral epithelium (figs. 4 and 20). In young gonophores the vacuolate cells possess one nucleus (fig. 3, *c*), but in older stages almost all these cells are binucleate, so that the villi, except for the tips of a few of the larger ones, are composed of binucleate cells. No mitoses have been seen, and the origin of the binucleate condition is not known. The cytoplasm of the mature vacuolate cells of the spadix is more dense and granular than elsewhere.

Hardy (1891) first pointed out for *M. cocksi* that "the whole spadix is a specialized structure for the absorption of nutriment from the somatic fluid of the blastostyle, which nutriment is doubtless largely derived from the stored material of the vacuolate cells through the help of the somatic fluid." This must also be true for *M. penola*. Here ciliated grooves between the blastostyle villi lead into the ciliated grooves between the villi of the spadix (pls. II and III, figs. 20 and 26 "f"), and the surface of the latter appears to be ciliated in many places. Thus a route is indicated for the transport of food material to the spadix. In both *M. cocksi* (Hardy, 1891) and in *M. penola* the peripheral spadix endoderm, which lacks nutritive spheres, shows many fine radial spaces in the cytoplasm (fig. 4). These may be concerned with

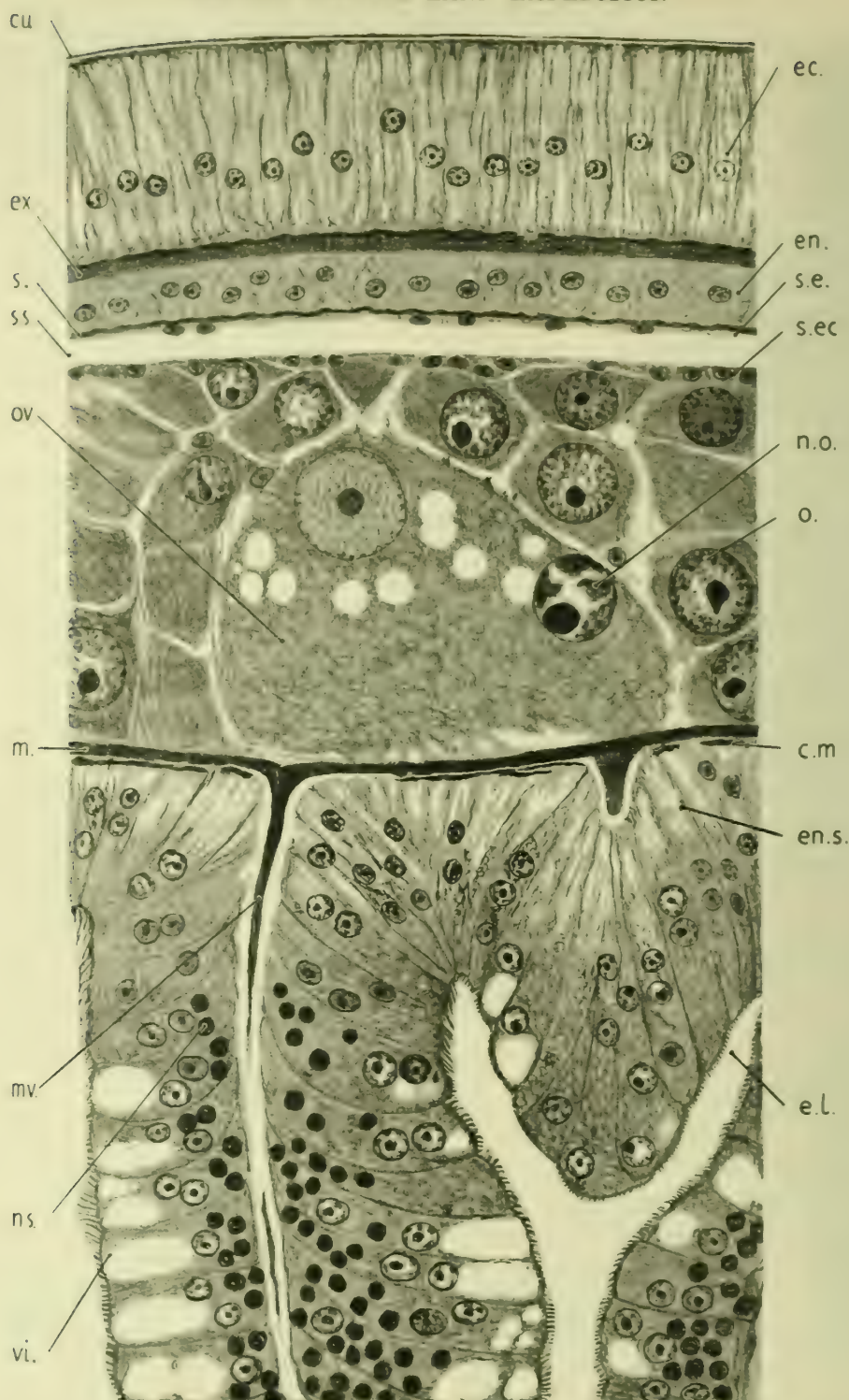


FIG. 4.—*M. penola*. Part of a section of gonophore "g.9" parasagittal to that shown in pl. II, fig. 20, and situated opposite the bracket marked "t.f.4". The gonophore wall is cut just to one side of the future velar perforation where the bell endoderm is excluded (see fig. 3, c, "s.ex."). The section passes through the definitive ovum which is in the process of uniting with the neighbouring oocytes; it shows one oocyte nucleus in its cytoplasm, which has not yet degenerated. The outer part of the endoderm with its villi is shown, see also pl. II, fig. 20. $\times 600$.

the transport of nutriment from the lumen of the spadix to the germinal epithelium.

The cells of the multilaminar ectoderm covering the spadix are at first equal in size. The oocytes below the surface layer of cells start to grow (fig. 3, c) and enlarge most rapidly near the endoderm and towards the apex of the spadix; they lie about six cells deep. In the gonophores of 0.5 mm. diameter and over (fig. 4) a single large ovum is present at the apex of the spadix, almost underneath the point of fusion of the bell mesogloea (fig. 3, c "s.ex."), where the velar opening will be formed (see below). The youngest ovum observed was in gonophore "g.6" (a little younger than "g.7" in pl. II, fig. 15) and measured $24 \times 15 \times 24 \mu$, the largest oocytes being not more than 12μ in diameter. Adjacent oocytes in the lower layers are incorporated into the ovum and their nuclei degenerate. In gonophore "g.9" (pl. II, figs. 15 and 20) the ovum measures $119 \times 75 \times 80 \mu$ and lies just to one side of the future velar opening (fig. 4). No older ova have been seen.

A velar perforation of the bell is formed in mature gonophores of *M. australis* and *M. harrisoni* (Briggs, 1928, 1929, 1931), and a perforation is almost completed (fig. 9) in one gonophore of *M. capensis* described on p. 280. This gonophore is not quite mature, but it is much older than those at the "g.9" stage in *M. penola*. The younger gonophores of *M. capensis* exactly resemble those of *M. penola*, and it is probable that a velar perforation is formed in *M. penola* when the gonophore reaches an age intermediate between "g.9" and "g.10" (pl. II, fig. 15), and that the perforation is situated where the bell endoderm is interrupted by the fusion of the two layers of mesogloea (fig. 3, c, "s.ex."). It is unlikely that fertilization in *M. penola* occurs by way of the enteric spaces of the hydroid as it does in the hermaphrodite *M. cocksii* (see p. 286).

Gonophores of the age of "g.10" (pls. I and II, figs. 11 and 15) contain one actinula larva, and are stretched and degenerate in structure. The larvae are all orientated with the aboral end against the spadix and the oral end towards the position of the velar perforation. The long provisional tentacles of the actinula are coiled about the sides of the larva leaving the oral disk of the larva uncovered. These tentacles are visible through the stretched bell wall (fig. 11). The latter is entire, and its component layers can be recognized. Sections show a thickened zone in the distal part of the bell in which the two layers of mesogloea unite. The stretching of the tissue has obliterated further details. It is probable that this zone represents the closed velar perforation, the lips of which fused after entry of spermatozoa to the sub-umbrella space. The spadix is degenerate and flattened (pl. II, fig. 21) and no longer projects (as in fig. 20) into the subumbrella space, which is entirely occupied by the larva. Most of the endodermal villi of the spadix have been absorbed, and the remains are shrunken, devoid of food reserves, and deficient in cytoplasm (pl. II, fig. 21, "sp."). The mesogloea layer, which originally separated the germ cells from the endoderm, is exposed and adheres to the stretched egg membrane (fig. 21 "e.me.") which is now about 14μ thick and encloses the larva. The external layer of this membrane stains red and the major part of the membrane stains blue with Mallory's triple stain (pl. IV, fig. 34, "e").

Two of the older gonophores show the beginning of the process of liberation of the actinula (pl. I, fig. 11, "a.e."). One of these shown in the photograph is traced in fig. 5, a, so that the details can more easily be identified. The gonophore bell has

split and shrunk back, forming a rim of tissue "g.s." round the flat spadix. The tentacles of the actinula have become less tightly packed, and the larva is retained only by the egg membrane which is attached to the spadix mesogloea (pl. II, fig. 21, "e.me.") Finally this membrane breaks down and the actinula becomes free. The gonophore is then represented by a shrunk rim of tissue on the blastostyle, often with a central perforation leading to the enteric space through the disintegrated spadix.

The development of *male* gonophores on the young specimen is not quite the same as that of the gonophores on the large female specimen. The rudiment of the endodermal part of the gonophore (fig. 3, *a*, "r.") appears at the earliest stage as a simple diverticulum of the blastostyle endoderm, the lumen of the two being continuous. It is probable that this difference between the male and female gonophores is not a sexual or a permanent one, but that it is connected with the great size difference of the two specimens and of their blastostyles (figs. 5, *a* and pl. I, fig. 10). The thin blastostylar endoderm of the small immature male allows the gonophore rudiment to be formed as in small species such as *M. cocksi* (Benoit, 1925), but in the large female specimen of *M. penola* the blastostylar endoderm is much thicker, and the endodermal gonophore rudiment is separated as a solid or almost solid vesicle which only later opens to the enteron of the blastostyle by growing through the thick endodermal epithelium. The further development of the male gonophores, as far as they are known, resembles that of the female.

GROWTH OF THE BLASTOSTYLE

The method of growth of the blastostyle is clearly indicated by the structure of its parts. On the blastostyle shown in pl. II, fig. 15, for example, the older gonophores are situated in progressively more distal positions. Fully developed tentacles are only found in the middle region of the blastostyle "t.2" where they are borne on small lobes; distal to these the blastostyle is almost bare of tentacles, and here lies the oldest actinula-bearing gonophore. The terminal bunch of lobes carries only degenerate tentacles "t.3" (see p. 264). Below the zone of fully formed tentacles, tentacle-bearing lobes are little developed. A younger gonophore "g.9" occupies a relatively bare zone, and near this gonophore and below it lies a zone of young tentacles, some projecting, as "t.1", and others, younger still, are represented by endodermal vesicles which cause no external elevation. The endoderm in the upper $\frac{1}{3}$ or more of the blastostyle is degenerate and devoid of food reserves (see p. 264) and the ectodermal cells near the apex of the blastostyle are laden with granules (see p. 258). It is probable that after the liberation of the actinula from gonophore "g.10" the distal part of the blastostyle, with its degenerate tentacles and gonophore remains, would be either absorbed or thrown off, and that the proximal part would then elongate and develop. The mature tentacles "t.2" would become terminal, gonophore "g.9" would take the place of gonophore "g.10", and the young tentacles "t.1" would grow and replace tentacles "t.2", and another gonophore proximal to "g.1" would be initiated. Other blastostyles indicate that considerably more than their distal $\frac{1}{3}$ may be lost. With the increase in diameter of the blastostyle, and with the formation of baggy tentacle lobes, the mesogloea layer must become stretched, and the external ridges, characteristic of the lower half of the blastostyle, become farther apart and

obliterated and absorbed. Growth of the blastostyle thus appears to take place from the proximal end, a condition unlike the main hydranth where growth in length occurs mainly from the oral end.

HYDRORHIZA

The hydrorhiza in the young individual is represented by adhesive tentacles arising from the base of the hydranth below the blastostyles. These tentacles are

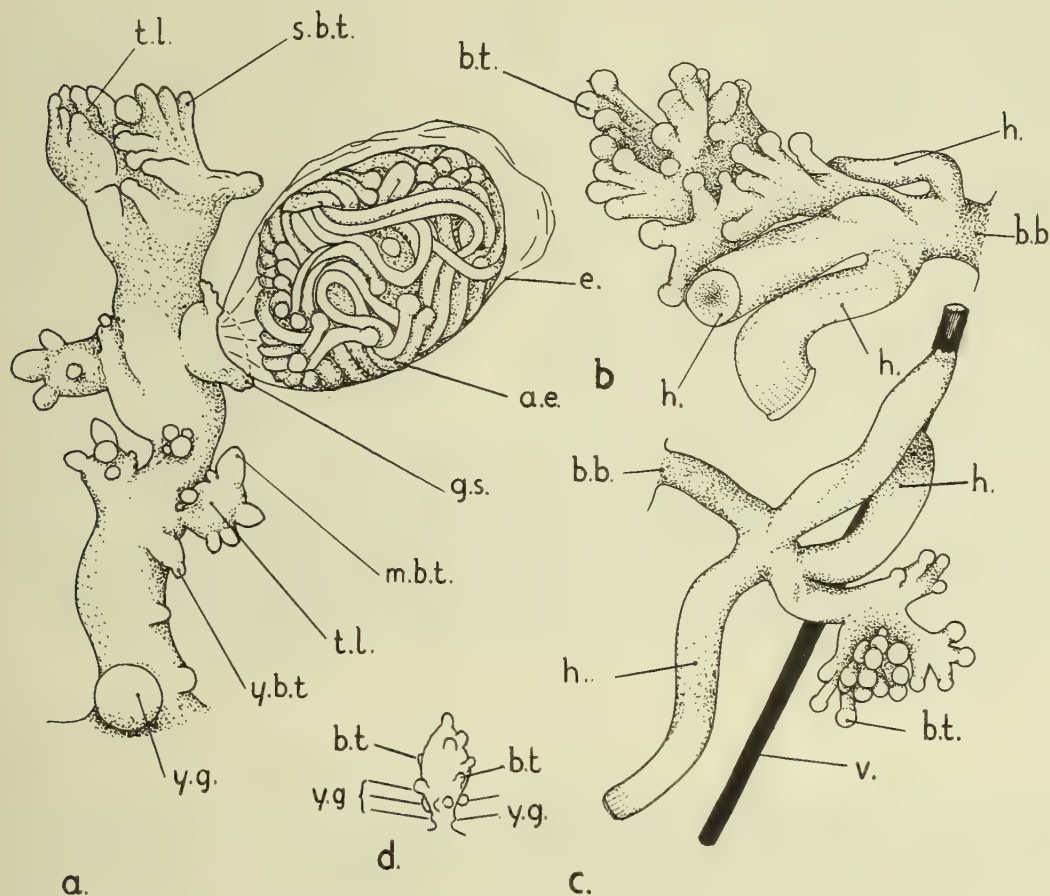


FIG. 5.—Figs. 5, *a-c*. Tracings of parts of *M. penola* shown in the photographs on pl. I, figs. 11 and 14, and orientated as in the photographs. Fig. 5, *a*, single blastostyle bearing an actinula larva retained only by the adhesion of the egg membrane to the spadix mesogloea, the gonophore wall having shrunk back “g.s.” $\times 4$. Fig. 5, *b*, blastostyle bearing three unattached adhesive hydrorhiza tentacles. $\times 4$. Fig. 5, *c*, blastostyle bearing one unattached hydrorhiza tentacle and two which are attached to the substratum (the rachis of a *Vigularia*). $\times 4$. Fig. 5, *d*, blastostyle from the immature male specimen. Similar blastostyles occur on the mature female specimen on the distal part of the blastostyle zone. $\times 4$.

from 1–8 mm. in length and 1 mm. or less in thickness, and they end in a flat disk. About 30 are attached to the substratum and all appear stretched, the longer tentacles being attached farthest from the animal and appearing to pull out the base of the hydranth. A few more adhesive tentacles spring from the hydranth near the more basal blastostyles and are unattached. In the adult specimen the adhesive tentacles

are larger and more numerous, reaching a length of 12 mm. and width of 2 mm., but the dimensions are variable. The tentacles arise from the base of the hydranth below the blastostyles, as in the younger specimen, but also from the spaces between the lower blastostyles and from these blastostyles themselves. Up to three adhesive

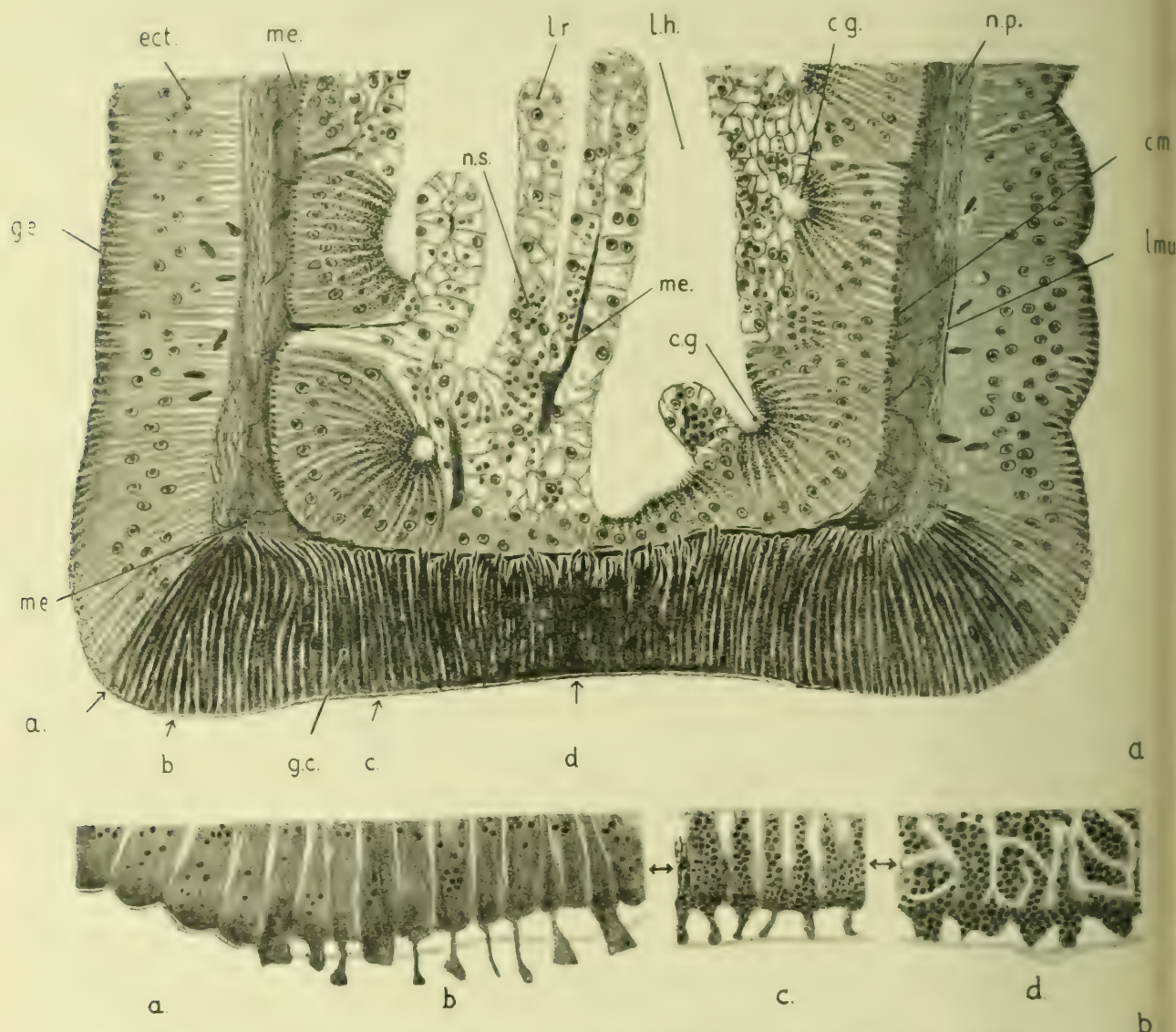


FIG. 6.—Fig. 6. *a*, shows a slightly oblique longitudinal section of a large adhesive hydrorhiza tentacle of *M. penola*. The grooves "c.g." and the ridges "l.r." are longitudinally orientated in the tentacle. $\times 140$. Fig. 6. *b*, shows the outer part of the ectodermal epithelium in the regions *a*, *b*, *c*, and *d*, in fig. 6, *a*. $\times 426$.

tentacles may be borne on the middle and basal part of one blastostyle. About 50 of these tentacles are attached to the horny axis of the *Virgularia* (pl. I, fig. 14), and a smaller number are free. In order to facilitate the identification of the structures shown in the photograph two of the blastostyles with their adhesive tentacles are traced in fig. 5, *b* and *c*. No perisarc is present on the unattached tentacle, but the

fixed tentacles adhere by means of a brown chitinous layer situated between the flat end of the tentacle and the substratum. In section the young tentacles resemble those of the smaller species *M. capensis* (fig. 7, c). A simple layer of columnar endodermal cells surrounds a central cavity communicating by a wide opening into the general enteron. The mesogloea layer is thick laterally, and compressed and denser across the flat terminal disk. The ectoderm over the flat end of the tentacle is formed of very long and narrow cells. Their bases are either sunk into, or project through, the mesogloea, and they are laden throughout with granules of various sizes which stain crimson with Mallory's triple stain and almost black with iron haematoxylin. Nematocysts are present in the ectoderm of the stem but not in the terminal disk.

The adult unattached tentacle differs from the above in its greater size and complexity of structure (fig. 6). The mesogloea of the stem is longitudinally furrowed on the ectodermal side. The ectodermal nerve plexus is very thick in the stem and forms a layer over the mesogloea which fills the valleys between the ridges of mesogloea. Ectodermal muscles are feebly developed, but the circular endodermal muscles form a substantial layer. This may be correlated with the need for an unattached tentacle to stretch out in search of its substratum. Strands of nerve fibrils pass through the mesogloea to reach the endodermal muscles.

The endodermal layer is grooved longitudinally. The angles of the furrows are formed by ciliated columnar epithelium, the distal parts of the cells being laden with granules staining scarlet with Mallory's triple stain, but remaining undifferentiated from the cytoplasm with haematoxylin, eosin, light green, etc. The ridges are bilaminar, being supported by a flange of mesogloea. They are composed almost entirely of vacuolate cells containing large vacuoles, nutritive spheres, and other inclusions, and usually showing two nuclei. These ridges and grooves are continued on to the inner side of the terminal disk (fig. 6).

The ectodermal epithelium of the stem resembles that of other regions of the body, and the sub-cuticular layer of granules is well developed. Over the terminal disk the darkly staining granular ectodermal cells are inserted into the mesogloea as in the young tentacle (fig. 6 and pl. IV, fig. 31, "e.i."). Their granules are most numerous near the mesogloea, but occur throughout the cells of the middle part of the disk. Certain differences can be seen among these cells which may be interpreted as changes associated with adhesion to the substratum. At the margin of the disk, where the granule-bearing cells merge into the stem ectoderm, the granules are fewer; here the surface cuticle is raised into a cone over each cell, the cytoplasm remaining in contact with the cuticle (position "a.", fig. 6); in most regions of the body the surface cuticle is flat (pl. III, figs. 22, 25 and 26). Towards the middle of the disk the surface cuticle becomes raised off the cells, each of which puts out one irregular cytoplasmic lobe. These lobes are largest in position "b." (fig. 6), and most of them here project right through the raised cuticle. Farther towards the middle the cytoplasmic lobes are smaller and lie below the raised cuticle (fig. 6, "c."), and the granules previously abundant in the middle and basal parts of the cells, now occur in the peripheral zone as well. In the central part of the disk, where the granules are largest and most abundant, the cytoplasm appears to be breaking up into irregular zones, and the peripheral parts of the cells appear to have fused forming a continuous sub-cuticular layer (fig. 6, "d."), bearing broad lobes which also contain granules.

It was not possible to section an attached tentacle or to remove one undamaged from its substratum. It is probable that the structure of an attached tentacle does not differ materially from those of *M. capensis* which have been sectioned in this condition. Here the terminal ectoderm is replaced by a chitinoid disk which is anchored to the mesogloea and adheres to the substratum (see p. 281 and fig. 7, *d*). The chitinoid disk shows the same staining properties as do the terminal ectodermal granules of the unattached adhesive tentacle. It is probable that in *M. penola* the substratum is first held by the lobes of cytoplasm which penetrate through the cuticle, and that a subsequent breakdown of the terminal epithelium and a fusion of the granules results in the replacement of the epithelium by the chitinoid disk. This is dove-tailed into the mesogloea where the bases of the epithelial cells penetrated this layer.

ACTINULA LARVA

The orientation of the actinula larva within the gonophore has been described (p. 269). Just before liberation the larva is pear-shaped and about 9 mm. long and 6 mm. wide (pl. IV, fig. 32). The mouth at the narrower end is not yet formed, and the oral pole is thickly beset with small tentacles 0.2 mm. long covering an area 1–2 mm. in diameter (pl. I, fig. 11 “t.o.”, and pl. IV, fig. 32). These small tentacles also clothe the upper $\frac{4}{5}$ of the larva, and among them arise about 40 long larval tentacles bearing rounded capitula. The more distal of these tentacles are about 30 mm. long and the proximal ones are shorter. The basal $\frac{1}{5}$ of the actinula is covered with about 30 short hydrorhiza tentacles (pl. II, fig. 21 and pl. IV, fig. 32).

The *oral and the short body tentacles* (pl. IV, figs. 30, 33 and 34, “s.t.”) have an ill-defined capitulum supported by a pad of short mesogloea fibrils. Nematocysts are most abundant distally. Heteronemes and stenoteles, slightly smaller than those of the adult, are abundant, desmonemes are few and small, and haplonemes are almost if not entirely absent. The endoderm surrounds a narrow central cavity, but this does not communicate with the main enteron, although the endodermal epithelia are continuous through a gap in the body wall mesogloea. The endoderm in the tentacle shows no regional differentiation as it does in those of the adult.

The capitulum of the *long larval tentacles* is well defined, and no pad of mesogloea fibrils is present. The capitulum is provided with a dense peripheral layer of atriches (pl. IV, fig. 29 “a.t.” and pl. III, fig. 24). These nematocysts do not occur elsewhere in either larva or adult. The insertions of their large cnidopods into the outer part of the mesogloea give the latter a striated appearance (fig. 24, “m.o.”). Among the atriches can be found a few heteronemes and fewer desmonemes and stenoteles. The endoderm surrounds a spacious cavity. Over the stem of the tentacle the ectoderm is produced into curious fluffy or dendritic processes (pl. IV, fig. 33, “ect.l.”), in which heteronemes and stenoteles are present but orientated in many directions. The stem endoderm is very thick leaving a narrow central lumen which is continuous with that of the main enteron. The inner parts of the endodermal cells contain many fine fuchsin-staining granules. An endodermal valve is situated at the base of the tentacle, where the columnar cells are supported by a flange of mesogloea (this mesogloea does not show clearly in the photograph, pl. IV, fig. 30, “v.l.”).

The *adhesive hydrorhiza tentacles* (pls. II and IV, figs 21 and 32, "h."), about 0.6 mm. in length, are miniatures of those of the smaller of the two adults. Their cavities communicate with the enteron, and their flat ends are covered by columnar ectodermal cells, full of fuchsin staining granules, which are anchored into the mesogloea. The bases of some of these ectodermal cells can be seen to be projecting right through the mesogloea in the section shown in fig. 31, "e.i.". The endoderm is a simple and regular epithelium (compare adult, p. 273, fig. 6), a condition doubtless associated with the small size of the tentacle. The inner parts of the endodermal cells are laden with fuchsin staining granules, as in the larval tentacles (pl. IV, fig. 31).

The enteric cavity of the actinula is traversed by numerous tongue- and ribbon-shaped villi about 0.5 mm. long (pl. II, fig. 21, "vi."). They are mainly composed of large vacuolate cells containing nutritive spheres, and their cytoplasm is scanty. The peripheral endoderm between the villi is composed of numerous small uninucleate cells with darkly staining cytoplasm (figs. 21 and 33, "p.e."). These cells doubtless give rise to the binucleate vacuolate cells, gland cells, etc., as the animal grows.

AGE AND RATE OF GROWTH

The methods of growth of the hydranth body and of the blastostyles and their appended organs have been described (p. 261 and p. 270), but the rate at which these processes take place is unknown. The condition of the two specimens of *M. penola*, however, enables various tentative suggestions to be made concerning the rate of growth and the age of the specimens.

There is probably a limited breeding season for the following reasons. The mature female shows a uniformity of condition among the larger gonophore bearing blastostyles. These each carry a series of gonophores, the largest of which are about 7.2 mm. in diameter and bear an actinula ready for liberation; on many of the blastostyles this actinula has already been liberated. The second largest gonophores are about 2.6 mm. in diameter, and contain a minute ovum and many oocytes. These would be expected to give rise to actinulae during the following breeding season.

It is also probable that there is only one breeding season in the year. The antarctic climate is unlikely to allow of more, but this cannot be proved. If this is so, then a year would elapse between the ripening of the gonophores of these two size groups ("g.10" and "g.9", pl. II, fig. 15), and for the distal part of the blastostyle to be replaced. Similarly the difference between gonophores "g.8" and "g.9" (fig. 15) would represent another year's growth. Since one gonophore only ripens annually on one blastostyle (only one exception to this generalization has been found, p. 264), it would take 9 years for the youngest gonophore on the blastostyle shown in fig. 15 to reach maturity; the gonophore "g.10" may be as much as 9 years old, and the female hydroid can be not less than 10 years of age.

Comparison of the gonophores of the two specimens (see p. 264) suggests that the older gonophores of the young male would take another 3 or 4 years to become mature. Relatively few of the male blastostyles bear gonophores, and when present they do not exceed 7 in number. Unless the gonophores arise more rapidly in the young hydroid than in the older animal, the young male (5.5 cm.) will be as much as 7 years old. Its growth would thus be slow, and it would be unlikely to attain the size of the

larger female specimen (85 cm.) by the time it was sexually mature. Thus the animal would start to breed at a smaller size than that of the female specimen. If this is true, then the species must continue to grow after sexual maturity.

Both specimens of *M. penola* appear to have been increasing in size at the time when they were collected. The female specimen already enormously exceeds the size of the hydranth of any other known hydroid. The size of the hydranth body of most hydrozoa, under favourable environmental conditions, appears to be constant for each species, and in actinozoa, such as sea anemones, there is a maximum size for each species, although the hydranth may reproduce sexually before it has attained this size. In *M. penola* there is reason to believe that sexual maturity is first attained at a size intermediate between those of the two known specimens (that is at a size exceeding those of temperate species), and that growth continues throughout many subsequent breeding seasons. There may be a maximum size for the hydranth of *M. penola*, but if there is, it does not appear to have been reached by the larger specimen in spite of the enormous dimensions; alternatively it is possible that under polar conditions of cold undisturbed waters there is no maximum size characteristic of the species, and that growth, without a compensating dedifferentiation (but with increasing complexity of structure, see p. 282), continues indefinitely, and results in a giant such as the larger specimen of *M. penola* with a hydranth body of 85 cm. The latter suggestion receives some support from the records of a large arctic species. Bonnevie (1899) describes fragments of *Myriothele* which are probably referable to *M. phrygia*; they were sexually mature but ranged in size from 4 to 40 cm. in length. If prolonged growth over many breeding seasons has led to an increase of size from 4 to 40 cm. it is unlikely that there is a fixed specific size in *M. phrygia*, such as is found in shallow water temperate and tropical hydroids. It is probable that growth in an extremely large hydranth may become slower and ultimately cease for mechanical or physical reasons.

MYRIOTHELE CAPENSIS sp. nov.

ORIGIN OF THE MATERIAL

Six specimens of *M. capensis*, obtained from the "Aquarium Rocks," East London, South Africa, on the 17th and 19th of July 1937, are present in the ecological collections of Professor Stephenson and Miss Eyre. All were attached to the alga *Ecklonia radiata*. One expanded specimen, measuring 17 mm., and one contracted specimen, are probably full sized, and bear female gonophores approaching maturity. Two expanded specimens 8 and 12 mm. long and one contracted individual are juvenile with small gonophores of undeterminable sex. The sixth specimen is much contracted and also young. The internal preservation of the material is not very good, and a detailed histological examination such as that carried out on *M. penola* was not possible on *M. capensis*.

GENERAL DESCRIPTION OF THE HYDROID (pl. I, figs. 12 and 13)

Tentacles cover the distal $\frac{9}{10}$ of the tubular hydranth, a zone about 15 mm. long and 1.5 mm. wide in the largest specimen. The proximal $\frac{1}{10}$ or less of the hydranth

bears a ring of about 20 cylindrical tentacle bearing blastostyles; they arise close together leaving no visible body surface between them. The hydrorhiza is in the form of about 20 adhesive tentacles which arise from the base of the hydranth. No perisarc is present, and the tentacles, when attached, are capped by a brown chitinous disk which adheres to the substratum. The species is dioecious, but only the mature female is known. Several specimens had recently swallowed copepods and small amphipods which were filling the enteron.

NEMATOCYSTS

The types of nematocyst found in *M. capensis* (fig. 1) correspond exactly with those of *M. cocksi* which have been described by Weill (1934). Stenoteles, desmonemes, and haplonemes of exactly the same size occur in the two species, and their staining reactions are those already described for *M. penola* (p. 256). Heteronemes are a little smaller than in *M. cocksi* and do not exceed $13.5\ \mu$ in length. The distribution of the nematocysts is recorded with the descriptions of the various parts. Those of the actinula have not been seen.

BODY WALL

The body wall is about $160\ \mu$ in thickness. The ectoderm calls for no particular comment; nematocysts are irregularly distributed, and desmonemes are the most frequent type. The cylinder of solid mesogloea is about $10\ \mu$ thick, and externally at intervals of about $16\ \mu$ longitudinal lamellae project from it into the ectoderm. These lamellae are about $80\ \mu$ deep, and many of them branch into two or three processes. Strap-shaped longitudinal muscle fibres are attached by their narrow edges to these lamellae, and nematocysts and other ectodermal elements lie in the grooves between the muscles. The endoderm provides circular muscle fibres over the inner side of the mesogloea. The endodermal epithelium is thrown into longitudinal villi. Near the mouth the villi are formed by elongation of the cells (fig. 7, *b*), but in the middle and lower part of the hydranth the villi are deeper and the epithelium is reflected forming a double-layered structure, but no flange of mesogloea passes into these villi. Gland cells are present, and in the middle and lower parts of the hydranth the cells composing the inner parts of the fold are laden with nutritive spheres. The poor preservation does not permit of more detailed description.

BODY TENTACLES

About 400 tentacles, 0.4 mm. in length cover the hydranth above the blastostyles. The capitulum is sharply demarcated from the stem, and an apical pad of mesogloea fibrils reaches a thickness of $87\ \mu$ (fig. 7, *b*). The nuclei of the capitular ectoderm lie at various levels, but the majority are half-way between the mesogloea and the surface. Almost all the nematocysts are situated in a dense peripheral layer. Desmonemes of various sizes with stout straight cnidopods are most numerous, haplonemes are frequent, and heteronemes and occasional stenoteles are present. The endoderm of the capitulum forms a darkly staining regular columnar epithelium. The lumen of the capitulum passes into that of the stem without constriction, and

no endodermal valve or mesogloea elaboration lies at this junction. The stem is almost devoid of nematocysts, the ectoderm is thin, and the endoderm forms an irregular epithelium of large lightly staining cells. Neither the lumen of the tentacle nor the endodermal epithelium passes through the mesogloea of the body wall which is continuous across the tentacle base (fig. 7, *b*). Proximally the endodermal lumen of the

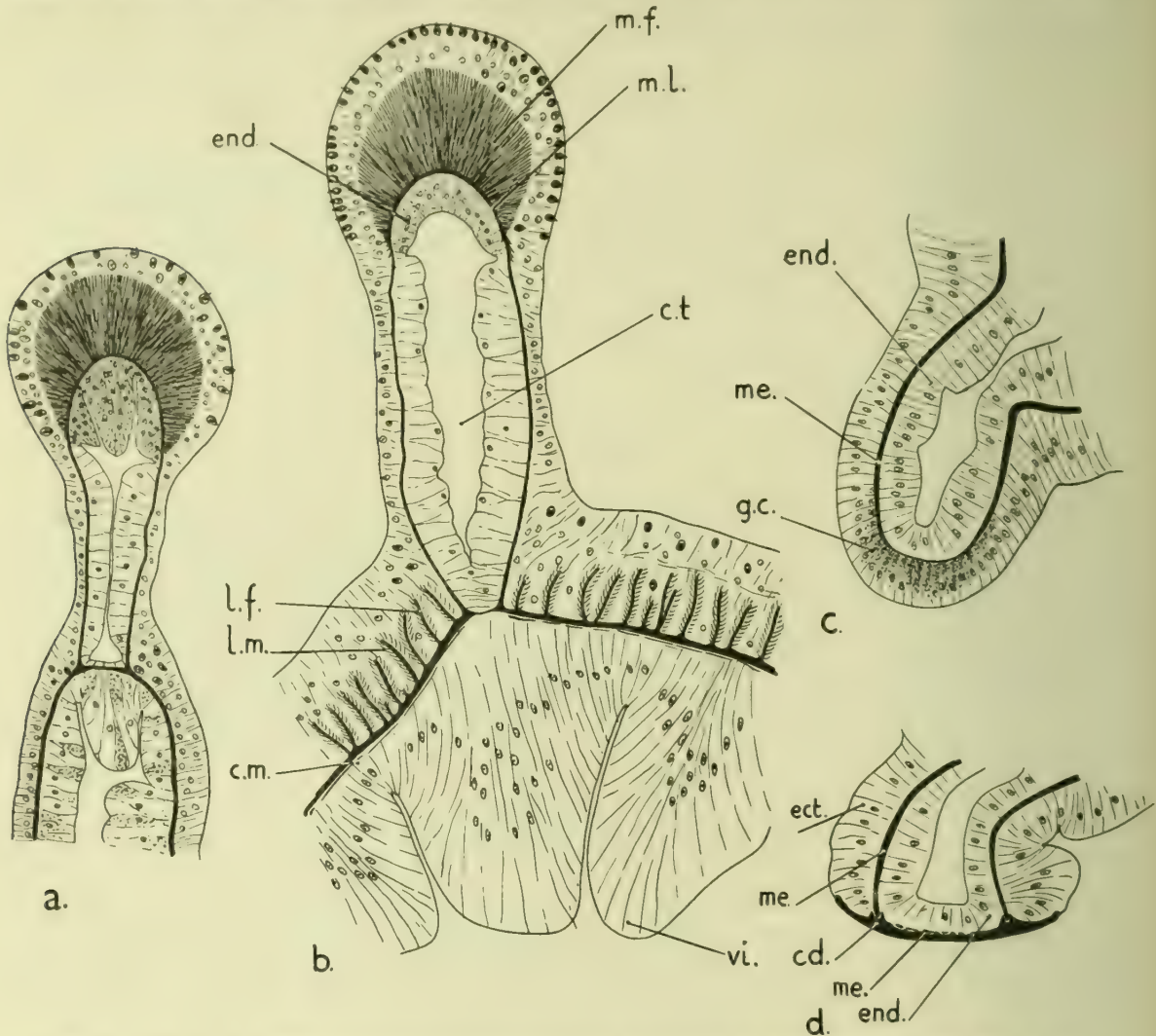


FIG. 7.—Fig. 7, *a*, shows a diagrammatic longitudinal section of a blastostyle tentacle and the tip of the blastostyle in *M. capensis*. $\times 150$. Fig. 7, *b*, shows a diagrammatic transverse section of the body wall and body tentacle near the oral end in *M. capensis*. $\times 160$. Fig. 7, *c*, shows a longitudinal section of an unattached hydrorhiza tentacle, and fig. 7, *d*, shows an attached hydrorhiza tentacle of *M. capensis*. $\times 140$.

tentacle is obliterated. No nematocyst nursery lies near the base of the tentacle as in *M. penola*, and nematocysts here may not be more numerous than elsewhere on the body wall.

BLASTOSTYLES

The proximal end of the hydranth may be simple or lobed, and bears a ring of about 20 cylindrical unbranched blastostyles 1.5 mm. in length (figs. 8, *b*, and pl. I,

figs. 12 and 13). Distally each blastostyle of the female bears about 5 capitate tentacles, and from the middle and basal parts spring about 4 sessile gonophores. Each blastostyle carries but one advanced gonophore. The wall of the blastostyle is simpler in structure than that of the hydranth. The ectoderm lacks nematocysts, except in the vicinity of tentacle bases; the mesogloea cylinder bears no external projections; and the endoderm is irregularly lobed and furrowed but possesses no villi.

Tentacles superficially resemble those of the hydranth body, but the darkly staining capitular endoderm is thickened forming a few conical projections which divide the lumen of the capitulum into narrow channels (fig. 7, *a*); this feature does not occur in any other described species. The endodermal lumen of the stem is very

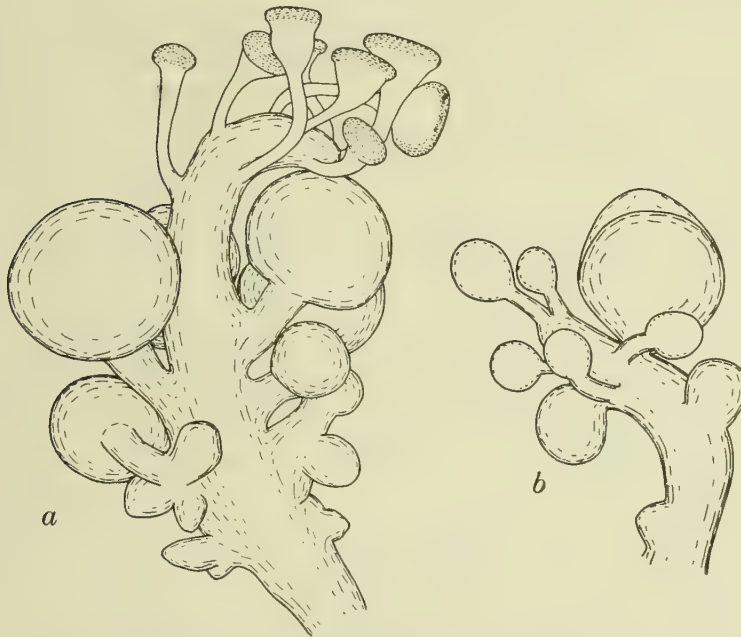


FIG. 8.—Outlines of female blastostyles of *M. australis* and of *M. capensis* to show the difference in the tentacles and in the insertions of the gonophores. $\times 28$. Fig. 8, *a*, *M. australis*, distally bearing trumpet-shaped tentacles and proximally stalked gonophores of different ages. Fig. 8, *b*, *M. capensis*, distally bearing knobbed tentacles and proximally four sessile gonophores of different ages.

narrow; it does not communicate with that of the blastostyle, but it extends to the base of the tentacle where the endodermal epithelium becomes thin over the blastostyle mesogloea (fig. 7, *a*). The nematocysts of the capitulum are fewer than on the hydranth body tentacles, but the same types are present and in the same relative abundance (fig. 1).

Only female *gonophores* are known, male individuals, if present in the collection, being immature. Only the distal gonophore on each blastostyle matures at a time, the proximally situated gonophores being younger. The largest gonophore is probably not quite full-sized, it has a diameter of 0.8 mm. and its broad base of attachment is about 0.25 mm. across. The structure of the sessile female gonophore resembles that of *M. penola* (p. 265), except that the size is smaller, fewer endodermal villi project into the spadix lumen, and the ectodermal musculature is almost if not entirely absent.

The development of the gonophores takes place as in *M. penola* (p. 265 and fig. 3). In gonophores up to 0.6 mm. in diameter there is no trace of a velar opening, the bell wall appearing as in fig. 3, c. In the largest gonophore present, of 0.8 mm. diameter, a velar opening is starting to develop. At the point where the two layers of mesogloea in the bell are confluent (see fig. 3, c, "s.ex."), the ex- and subumbrella ectoderm has become transformed as shown in fig. 9. Both epithelia are here thickened and an exumbrella invagination is formed over the solid disk of mesogloea. The subumbrella ectoderm below forms a disk of compact darkly staining cells surrounded by a rim of elongated cells. No later stage has been seen, but if the invagination "v.in" broke through the bell wall, a condition would result which would resemble the velar perforation described and figured by Briggs for *M. harrisoni* and *M. australis*.

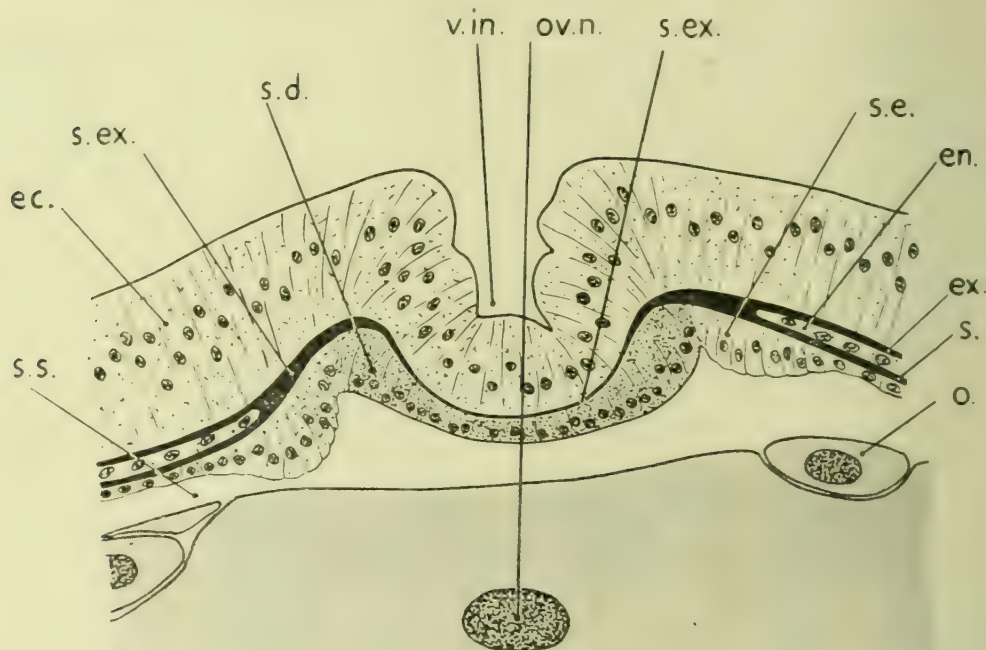


FIG. 9.—Sagittal section through the distal part of the female gonophore of *M. capensis* just before the velar perforation is made. $\times 105$. Compare with the region near "s.ex." in fig. 3, c, a younger stage of *M. penola*, and with pl. 34, fig. 5, Briggs, 1928, an older stage of *M. harrisoni*.

(1928, pl. 34, fig. 5, and 1929, pl. 43, fig. 2). It is probable that an open velar perforation occurs in both male and female gonophores of *M. capensis*, and that fertilization takes place through this pore. This opening in the female gonophore may then close, as it must do in *M. penola*, during the period of development of the actinula larva.

The development of ova in *M. capensis* takes place by the second method described by Benoit (1925) for *M. cocksi*. When the gonophore reaches a diameter of 0.4 mm. and the oocytes, $24\ \mu$ in diameter, lie about three cells deep, three or four ova of larger size become differentiated and grow at the expense of the neighbouring oocytes. One gonophore of 0.68 mm. contained four ova 0.27–0.3 mm. in diameter, and the largest gonophore (referred to above) contained three ova of 0.5 mm. diameter, the

remaining oocytes being 0.04 mm. across. Older stages have not been seen, but the mature gonophore probably contains one ripe ovum, as in *M. cocksi* and other species.

HYDRORHIZA

The hydrorhiza is in the form of 20–30 short adhesive tentacles springing from the basal surface of the hydranth below the blastostyles (pl. I, fig. 12). The tentacles arise close together and rarely exceed 0.4 mm. in length, many being much shorter. When attached to the substratum each tentacle is capped by a weakly convex chitinoid disk, 0.25 mm. in diameter, which adheres to the substratum. The tentacles radiate outwards from the hydranth and appear to pull out its base over as wide an area as possible. Longitudinal sections through unattached and attached tentacles are shown in figs. 7, *c* and *d*. Columnar ectodermal and endodermal epithelia are separated by a simple layer of mesogloea bearing no external projections. Muscles are not strongly developed; and the internal cavity communicates directly with the main enteron without any basal constriction. In the unattached tentacle (fig. 7, *c*), the apical mesogloea is thinner than elsewhere, and the apical ectodermal cells contain many granules which stain red with fuchsin. In the attached tentacle (fig. 7, *d*), which was pulled off its substratum before sectioning, the apical ectoderm has disappeared, and a chitinoid disk with the same staining properties as the ectodermal granules, has taken its place, and has presumably been formed from the granules previously in this position. Just within the rim of the chitinoid disk its substance is thickened and closely attached to the stem mesogloea, which is sunk into a groove in the disk. The terminal sheet of mesogloea within the middle of the chitinoid disk also adheres closely to the latter, and the disk appears to be dove-tailed into the mesogloea in many places.

DISCUSSION

Different species of *Myriothela* occupy parallel types of environment in both southern and northern hemispheres. There are small shallow water forms attached to rocks or seaweed, *M. cocksi* (50 mm.) in the northern, and *M. capensis* (17 mm.) and *M. harrisoni* (15 mm.) in the southern hemispheres. Larger forms occur in deeper and colder water, *M. gigantea* (300 mm.) and *M. phrygia* (400 mm.) have been dredged from over 2000 m. by the Norwegian North Atlantic Expedition 1876–88, and *M. austro-georgiae* (300 mm.) has been collected from various depths below 20 mm. by four antarctic expeditions. Both *M. austro-georgiae* and *M. penola* (850 mm.) have been found torn from their substrata and floating on the surface of the sea, the former in a hole cut in the ice over 20–30 fathoms (Scottish National Antarctic Expedition), and the latter among ice-floes in a shallow creek. The hydrorhiza of *Myriothela* if pulled from its substratum, cannot affect a new attachment, but any unattached adhesive tentacles might adhere to a new substratum, and in any case actinula larvae may be liberated from the floating hydroid which may possibly live in this position for a long time.

The only other hydroid known to attain great size is *Branchiocerianthus*, and this genus is also found only in cold water. Stechow (1909) has suggested that *Branchiocerianthus* needs absolute quiet water in which to attain large size, and this may be

true also for the larger species of *Myriothela*. *Branchiocerianthus* has only been collected from the cold abysmal regions of the warmer seas (Broch, 1918, p. 176), while giant *Myriothelas* have been found in the cold seas of the north Atlantic and Antarctic regions, either at great depths or in sheltered water.

The preservation of such a large animal as *M. penola* whole in formalin has been remarkably good, and has made possible a thorough examination of much of its structure. The good fixation may be due to the low temperature at which it was fixed and to the care with which Dr. Bertram narcotized and preserved the animal. *M. capensis*, only $\frac{1}{50}$ the size of *M. penola*, and also preserved in formalin, but in a warmer climate, is very poorly preserved for histological purposes.

M. penola, 850 mm. long, is a giant among hydroids, and is more than double the length of the largest known species of the genus. This great size has led to many elaborations of structure not found in smaller species, and these features are doubtless due to the impossibility for an organism to increase in size beyond certain limits without alteration of both the structure and the proportions of its parts. Features which may be so interpreted occur throughout the organism and its large actinula, and some of these will be mentioned below.

The height of *M. penola* is 50 times that of *M. capensis*, but the tentacles of *M. penola* are not enlarged proportionately; they are only 5 times the length of those of smaller species, and the capitulum is only about $2\frac{1}{2}$ times as wide as in *M. capensis*. This larger tentacle has a more complex and mechanically stronger structure (see p. 259), but its nematocysts are only slightly larger than those of smaller species.

Some dimensions of full-sized specimens of four species of *Myriothela* are given in Table 1. The body wall mesogloea of *M. capensis* and *M. penola* is shown in pl. III,

TABLE 1

SMALL SPECIES				LARGE SPECIES		
	<i>M. cocksi</i>	<i>M. capensis</i>		<i>M. austro-georgiae</i>	<i>M. penola</i>	
Length of body	50 mm.	17 mm.		300 mm.	850 mm.	
Width of body	1.5 mm.	1.5 mm.		12 mm.	middle tentacular region 12 mm.	lower tentacular region 30 mm.
Thickness of body wall. . .	140 μ	160 μ		300 μ	180 μ	360 μ
Thickness of basal sheet of mesogloea	15 μ	10 μ		20 μ	45 μ	90 μ
Depth of external processes of mesogloea	30 μ	80 μ		70 μ	30 μ	120 μ
Distance apart of external processes of mesogloea	6 μ	18 μ		12 μ	9 μ	40 μ

figs. 27 and 28, and that of *M. austro-georgiae* in pl. 2, figs. 3 and 4, Jäderholm, 1905. The thickness of the body wall is greater in the larger species, but the thickness does not increase proportionately with the external dimensions of the body; thus in *M. penola* the body wall is only a little thicker than in *M. austro-georgiae*, an animal less than half the length. The body wall, is, however, more strongly constructed in the two larger species, where the amount of mesogloea is greater. The proportion of mesogloea in the form of a solid sheet may be greater (see figs. 27 and 28), and where the external mesogloea lamellae are shallow, they are set closer together, so providing plenty of surface for muscle attachment. In parts of *M. penola* where these lamellae are shallow they are much thicker than in smaller species, and must thus be stronger. The variations in the mesogloea layer in different parts of the body of *M. penola* are also seen to be correlated with the size of these parts and their requisite support. In the lower and middle regions of the blastostyles, for example, the basal sheet of mesogloea is only 10–20 μ in thickness and the external lamellae project about 20–30 μ , whereas in the body the basal sheet is 45–90 μ thick and the external lamellae project 30–120 μ . These proportions of mesogloea in the blastostyle of *M. penola*, moreover, closely resemble those in the body wall of *M. australis*, an animal in which the whole hydranth is of about the same size as a single blastostyle of *M. penola* (compare pl. III, fig. 26, with Briggs, 1928, pl. 34, fig. 4).

The depth of the endodermal villi of large and small species appears to be proportional to the diameter of the body, but the thickness of the villi in larger forms is only about double that in the smaller forms, and the villi are correspondingly more numerous in the larger species. The apical cells, which may be concerned with the absorption of food, only form the extreme edge of each villus in small species such as *M. cocksi* (Hardy, 1891) and *M. australis* (Briggs, 1928), but in *M. penola*, where a relatively larger absorptive area would be expected, a larger part of each villus is formed by these cells (see p. 259).

The evidence for the view that the “metabolic activities of different parts of the endoderm are brought into relation with one another through the agency of the somatic fluid” which fills the enteric space was first put forward by W. B. Hardy (1891) working on *M. cocksi*.¹ He showed that this fluid must convey stored nutriment from one part of the body to another, and he followed the breakdown and utilization of the nutritive spheres. He suggested that the fluid was “circulated by the active movements of the animal, which include the extension and retraction of the blastostyles, and possibly by cilia, which appear to be borne here and there by the endodermal cells.” These suggestions are undoubtedly true also for *M. penola*. The blastostyles of this species are the largest known in the genus, and their more elaborate structure is doubtless associated with the need for more efficient circulation of the enteric fluid. The close set villi separated by ciliated grooves do not occur in the blastostyles of smaller species, where the endoderm is only slightly lobed and furrowed, and these ciliated grooves must provide direct and rapid channels for the transport of fluid from the general enteron to the cavities of the spadices of the gonophores.

Two other features correlated with size have already been mentioned. The internal structure of the hydrorhiza tentacles becomes more complex with increase

¹ The name *M. phrygia* has been used by Hardy and others for the British species of *Myriothela*.

of size (p. 271); and the unusual details of the development of the gonophore rudiment in the larger specimen is probably due to the size of the blastostyle (pp. 265 and 270).

The large size of the *actinula* of *M. penola* probably accounts for the structural differences between this larva and those of smaller species. Tentacles of all kinds are relatively more numerous and much more closely set, and the oral zone of crowded short tentacles is not seen in the small actinulae of *M. cocksi* and *M. phrygia* (Allman, 1875, pl. 38, fig. 6; Sars, 1877, pl. 2, figs. 35 and 36), or in the newly fixed young of *M. australis* and *M. harrisoni* (Briggs 1928, pl. 32, fig. 2 and pl. 33, fig. 3). The long larval tentacles which are later absorbed are locomotory in function, "the terminal capitula being used as suckers of attachment" (Allman, 1875). In *M. penola* these provisional tentacles have the remarkably wide spread of 65 mm., and their abundant nematocysts, well anchored to the mesogloea and probably adhesive in nature, are fitted to hold the large body of the actinula to any suitable substratum that is encountered. In small actinulae, such as those mentioned above, the aboral end of the body forms a single adhesive or suctorial disk. In *M. penola*, the precociously developed hydrorhiza tentacles covering the base of the larva provide a large number of potential points of adhesion; these will enable a much stronger attachment to be made than would be possible with a single suctorial disk. Endodermal villi are also precociously developed, they are absent from the small actinula of *M. cocksi*, where they only appear later in the growing hydranth.

It has been suggested (p. 275) that *continuous growth from growth zones* recognizable on the blastostyles and on the body of *M. penola* has led to the absence of specific size and to the large dimensions of the mature specimen of this species. A continuance of growth without compensating dedifferentiation may take place over very many years. Bidder (1932) has pointed out that "indefinite growth is natural", but indefinite increase in size, such as shown by the female plaice, is rarely seen. In the great majority of organisms, for a variety of reasons, growth is regulated and not indefinite, and specific size results.

Stechow (1909) has shown that in the giant solitary hydroid *Branchiocerianthus* growth is persistent, and so there is no specific size as in smaller colonial hydroids, where budding follows the attainment of the specific size. The growth of *Branchiocerianthus* is carried out by a unilateral growth zone on the hydranth body which continually adds new tentacles, blastostyles, radial canals, etc., to either side, and the hydranth body thus becomes bilaterally symmetrical. This remarkable method of growth is correlated with the enormous size of *Branchiocerianthus* (Stechow, 1909). Thus in both the known genera of giant solitary hydroids specific size appears to be absent, and continual growth occurs from definite growth zones, the details of which are quite different in the two genera. The largest *Branchiocerianthus imperator* known measures 7 ft. 5½ in. (2235 mm.), but the hydrocaulus contributes 7 ft. 4 in., the hydranth body being only 1½ in. long. In *M. penola* however, the hydrocaulus is absent and the hydranth body has attained the great length of 2 ft. 8½ in. (850 mm.) in the largest known specimen.

The occurrence of *binucleate endodermal cells* is remarkable, such a condition being so unusual in any animal tissue. Binucleate nephrocytes and oenocytes occur

in some insects, and the ovarian tube in *Pediculus humanus* shows a binucleate epithelium (Keilin, 1917, 1930). Hardy (1891) recorded binucleate vacuolate cells in *M. cocksi*, a feature which can readily be confirmed. Briggs (1928, 1930) noted that some of the vacuolate cells of *M. harrisoni* but not those of *M. australis* are binucleate. In *M. penola* the greater part of the endoderm is composed of binucleate vacuolate cells, but the actively growing parts of the endoderm are uninucleate (see endoderm of body wall, but not villi, of the actinula, p. 275, and of the wall of the spadix, p. 267). These uninucleate undifferentiated cells presumably give rise to the binucleate cells. This binucleate condition may be characteristic of most species of the genus, irrespective of the size of either the whole animal or of its component cells.

The type of *hydrorhiza* which is composed of adhesive tentacles growing from the base of the hydranth occurs in *M. phrygia* and *M. verrucosa* in the northern hemisphere and in *M. australis*, *M. capensis*, *M. penola*, and *M. austro-georgiae*, in the southern hemisphere. Of the northern species, the hydrorhiza of *M. phrygia* is described and figured by M. Sars (1877), and in a mature specimen, 1½ in. long, consisted of 10 fixed and 9 free tentacles, the former adhering by flat horny extremities. In a larger specimen 7 cm. long which I have examined¹ the adhesive tentacles are more numerous. They resemble those of the southern hemisphere species except that many of them appear to have shrunk in diameter, so leaving the terminal disk of attachment appearing much wider than the stem. The overlapping of the hydrorhiza and blastostyle bearing zones in *M. penola* is a feature which has not been described in other species. It also occurs to a minor degree in a specimen of *M. phrygia* in the Bergen Museum, where three of the proximal blastostyles bear adhesive tentacles arising from their lower parts.

The method of formation of the chitinoid disk on the hydrorhiza tentacles is a most unusual one. In invertebrates the integuments, apodemes, peritrophic membranes, etc., are usually formed by a secretion which lies outside the epithelium or gland cell (Yonge, 1932, Wigglesworth 1930, 1933, Manton 1928, 1938, etc.). The formation of a chitinoid layer in *Myriothela* by the destruction of an epithelium, which is replaced by material originally intracellular, in such a way that the disk is linked with the mesogloea, is doubtless associated with the necessity for the permanent adhesion by the tentacle to be strong. In the Alcyonaria a strong and permanent adhesion to the substratum is obtained either directly by the mesogloea or by a horny axis; in the former case the ectodermal epithelium disappears at this junction, and in the latter case the axial epithelium, if it is present, lies on the surface of the axis away from the substratum.

The development of the *gonophores* of *Myriothela* has been studied most extensively on *M. cocksi*, a complete and beautifully illustrated account being given by Benoit (1925) who has correlated the previous partial descriptions by Allman (1875), Korotneff (1879, 1888), and Hardy (1891). The very early stages described by Benoit have not been seen in *M. penola*, but the development recorded above differs in no essential manner from the corresponding stages of *M. cocksi*, a minor difference being correlated with size (see p. 270).

¹ By courtesy of Dr. Brinkmann.

The presence or absence of a velar perforation on the gonophore in different species of *Myriothela* probably depends on the method of fertilization of the eggs. In the hermaphrodite *M. cocksi* the gonophore wall remains entire. Benoit (1925) has shown that fertilization takes place at night, the sperm passing from the male gonophore by way of the endodermal spaces to the spadix of the female gonophore, and then through the endodermal epithelium to reach the ripe ovum. Development begins within the closed gonophore, and the embryo later escapes by a rupture of the wall which starts at the point where the endodermal layer is interrupted, that is, at a point corresponding with the velar opening. In *M. australis*, *M. harrisoni*, *M. meridiana* (Briggs, 1928, 1929, 1938), *M. capensis*, and almost certainly in *M. penola* a velar perforation is formed when the sperm and ova reach maturity. Sperm are probably liberated through this opening and gain access to the female gonophore thereby. That such an opening has not been described in other dioecious species may be due to suitable stages not having been available for examination; of the six specimens of *M. capensis* which have been inspected, only one gonophore on one specimen is old enough to show the formation of this opening, and on the two specimens of *M. penola* all the gonophores are either too old or too young to exhibit this feature. A closure of the velar opening of the female gonophore after fertilization has not been recorded in species other than *M. penola*, but this again may be due to the absence of available material of a suitable age. In *Tubularia* the velar perforation remains open during the development of the actinula, but the gonophore here contains several embryos of different ages, and the velar opening must remain open both for liberation of actinula and for intake of sperm.

Benoit (1925) described the mature ovum of *M. cocksi* developing by two alternative methods. Either one oocyte situated on the axis of the gonophore grows by progressive fusion with its neighbours, those oocytes close to the spadix being absorbed first; or several plasmodial areas (up to ten) are formed by fusion of oocytes near the spadix. These all grow for a time, but the one situated on the axis of the gonophore alone persists and unites with the others to form the mature ovum. All the gonophores bearing definitive ova which have been sectioned show the former type of development in *M. penola* and the latter type in *M. capensis*. *M. australis* and *M. harrisoni* resemble *M. capensis* in this respect.

In *M. penola* the development of the single ovum starts relatively earlier than the several ova of *M. capensis*. The ovum of *M. penola* becomes differentiated when the gonophore is less developed and the surrounding oocytes only half the diameter of those at a similar stage in *M. capensis*. This may be associated with the volume of the mature egg of *M. penola* being about 1000 times greater than that of *M. capensis*.

The genus *Myriothela* in the northern hemisphere comprises six species, and the desirability of retaining all these forms within a single genus was advocated by Bonnevie (1899). Since this date six southern hemisphere species have been found, *M. austro-georgiae*, *M. penola*, and *M. meridiana* from antarctic waters, *M. australis* and *M. harrisoni* from Australian, and *M. capensis* from South African coasts. The desirability of including the southern forms within the original genus has been questioned. I have examined four southern and two northern hemisphere species, and

from the available information there appears to be no character common to the southern hemisphere species which would justify their separation from the northern forms.

The nematocyst armature, where known, is similar in southern and northern species. (Of the previous descriptions of nematocysts of species of *Myriothela*, only that given by Weill (1934) for *M. cocksi* can be considered complete.) It has been emphasized by Weill that the cnidomes of the various genera of Gymnoblastera are distinctive. The similarity between the northern and southern species of *Myriothela* in this respect is even greater than it is within the genus *Tubularia*.

The structure of the body tentacles varies little among the species of *Myriothela*, beyond modifications correlated with size (see p. 282). The blastostyle tentacles, if present, vary greatly, but in no significant manner, except that the development of flat-topped, trumpet-shaped capitula appears to be a feature characteristic of the known Australian species.

The endodermal villi show some variations correlated with size (see p. 283), but the absence of a flange of mesogloea in the villi of *M. cocksi*, *M. capensis*, *M. phrygia*, and *M. minuta*, and its presence in those of *M. australis*, *M. harrisoni*, *M. austro-georgiae*, and *M. penola* is connected neither with size nor with geographical distribution.

The hydrorhiza shows three forms among the northern species (see Bonnevie, 1899), and two of these are also shown by the southern species (see Table 2). The claspers of the northern *M. cocksi*, previously considered to be unique, are probably comparable to part of the hydrorhiza of forms such as *M. penola* in the southern hemisphere (Manton, 1941).

Finally the cryptomedusoid gonophores are of much the same structure in southern and northern hemisphere species. The presence or absence of a velar perforation is associated with the method of fertilization (see p. 286). The southern hemisphere species are dioecious, as are the northern *M. phrygia*, *M. venucosa* and *M. gigantea* (Bonnevie, 1899), but *M. cocksi*, and possibly others are hermaphrodite.

A table is given below summarizing the main characters of the southern species of *Myriothela*. This table may be compared with that given by Bonnevie (1899) for the northern hemisphere species. In structure and habits *M. capensis* superficially resembles *M. australis*, but their blastostyle tentacles and the insertions of their gonophores are unlike. The blastostyles of these two species are shown in fig. 8, and a section of a blastostyle tentacle of *M. capensis* in fig. 7, *a*, may be compared with that of *M. australis* (Briggs, 1928, pl. 39, fig. 2).

Bonnevie (1899) has summarized the views previously expressed concerning the relationships of the Myriothelidae, some authors suggesting that the family is closely related to the Corynidae and others to the Tubularidae. Weill (1934) has discussed the taxonomic value of the cnidome in the coelenterates; he has reviewed the classification of the gymnoblastic genera, and on the basis of the cnidome he has proposed a more rational grouping. A cnidome consisting of four types of nematocyst and including desmonemes and stenoteles, occurs only in the Myriothelidae, Tubularidae and Pennaridae (see Weill, 1934, and Russell, 1938), while in the hydroids once grouped in the family Corynidae the cnidomes are different, and consist of only two or three types of nematocyst. Thus the suggested affinity between *Tubularia*, *Ectopleura*, etc., and *Myriothela* is supported.

TABLE 2
SOUTHERN HEMISPHERE SPECIES OF MYRIOTHELA

Species.	Size.	Hydrorhiza.	Body Tentacles.	Blastostyles.	Blastostyle Tentacles.	Gonophores.	Locality.
<i>M. austro-georgiae</i> Jäderholm, 1905	300 mm.	Adhesive tentacles on base of hydranth, perisarc absent.	Covering whole hydranth.	Unbranched, 3 mm. long.	One long terminal tentacle, sometimes smaller ones also.	Sessile. ♀ 22 mm., < 6 per blastostyle. ♂ 1.5 mm., < 10 blastostyle.	South Georgia, Kerguelen Isl., Graham Land.
<i>M. penola</i> , n.sp.	850 mm.	<i>Ditto</i>	Covering hydranth above blastostyle bearing zone only.	Lobed, 22 mm. long.	Many knobbed tentacles on the blastostyle lobes.	Sessile. ♀ 8 mm., < 10 per blastostyle. ♂ ?	Graham Land.
<i>M. australis</i> Briggs, 1928	30 mm.	<i>Ditto</i>	<i>Ditto</i>	Unbranched, 3 mm. long.	About 8 trumpet-shaped tentacles.	Stalked. ♀ 1 mm., < 12 per blastostyle. ♂ less than 1 mm. < 15 per blastostyle.	Marouba Bay, New South Wales.
<i>M. capensis</i> n.sp.	17 mm.	<i>Ditto</i>	<i>Ditto</i>	Unbranched, 2.5 mm. long.	About 5 knobbed tentacles.	Sessile. ♀ 0.8 mm., < 5 per blastostyle. ♂ ?	Port Elizabeth, South Africa.
<i>M. meridiana</i> Briggs, 1938.	30 mm.	?	<i>Ditto</i>	Branched, 7 mm. long.	Absent.	Stalked. < 50 per blastostyle.	Macquarie Isl.
<i>M. harrisoni</i> Briggs, 1928, 1930	15 mm.	Expanded processes from basal cylinder, whole covered by perisarc.	<i>Ditto</i>	Unbranched, 1 mm. long.	A single terminal trumpet-shaped tentacle.	Sessile or shortly pedunculate. ♀ 0.9 mm., < 2 per blastostyle. ♂ 0.45 mm., < 7 per blastostyle.	Bulli, New South Wales.

I am indebted to Dr. A. F. W. Hughes, Dr. J. P. Harding, and Dr. I. Manton for taking the photographs reproduced in the plates, and to Dr. E. A. Briggs and Dr. A. Brinkmann for kindly lending specimens of *M. australis* and *M. phrygia* respectively.

SUMMARY

(1) Two new species of the hydroid *Myriothela* are described: *M. penola*, a giant antarctic form, and *M. capensis* a small species from the coast of South Africa. For a summary of characters, see Table 2, pp. 288.

(2) The great size of *M. penola* is correlated with many structural features not seen in smaller species. Examples of such features are noted from the body tentacles, the mesogloea of the body wall and of the blastostyle, the endodermal villi of the hydranth and of the blastostyle, the hydrorhiza tentacles, etc. Characters of the actinula larva also correlated with size are the large number of the oral and body tentacles, the great length and the number of the provisional larval tentacles, and the precocious development of the hydrorhiza tentacles and endodermal villi which are present in the larva before its liberation.

(3) Provision is made in *M. penola* for direct transport of enteric fluid (and thus of food material) by ciliated grooves, situated between close-set blastostyle villi, which lead from the general enteron to the spadices of the gonophores.

(4) The method of growth of *M. penola* is described. Increase in length of the body takes place most actively at the oral end. Body tentacles become dedifferentiated and absorbed progressively in the post-oral positions, and finally disappear at the aboral end of the tentacle bearing zone. The blastostyle bearing zone grows in length at its oral end at the expense of the tentacle zone, young blastostyles growing in place of the absorbed tentacles.

(5) The blastostyles of *M. penola* are relatively larger than those of any known species and they show a zoning associated with growth. Increase in length occurs at the basal end where young tentacles and young gonophores are formed. Mature tentacles and gonophores lie in the middle region, and the terminal tentacles and blastostyle wall are degenerate in structure. After the liberation of an actinula larva the remains of the gonophore and the distal degenerate parts of the blastostyle are either absorbed or cast off.

(6) Only one gonophore on each blastostyle of *M. penola* matures at a time. All the older gonophores are at one of several distinct stages of development, which are uniform on all blastostyles bearing gonophores. There is a limited breeding season, and if this is annual, the differences between these gonophores represent one year's growth.

(7) Both *M. penola* and *M. capensis* are bisexual. There is evidence that a velar perforation is formed in both species when the genital products are ripe. The perforation closes after fertilization in *M. penola* and possibly in other species also.

(8) The development of the gonophores of *M. penola* and of the ova of *M. penola* and *M. capensis* are described.

(9) The method of attachment of the hydrorhiza tentacles to the substratum is described in *M. penola* and *M. capensis*. Adhesion is first made by the surface of the terminal ectodermal cells. Then intracellular granules in these cells unite and the cells break down. The epithelium is thus replaced by a chitinous disk, formed from the granules, which adheres to the substratum and is dove-tailed into the mesogloea of the tentacle.

(10) Some tentative suggestions are made concerning the age and rate of growth of *M. penola*. It is probable that growth is slow and that it continues over very many breeding seasons. It is also possible that giant size is attained under polar conditions owing to the absence of a constant specific size, and an indefinite continuance of growth from fixed growth zones without compensating dedifferentiation.

(11) A review is given of the southern hemisphere species of the genus *Myriothela*. It is considered that there is no justification for a separation of the southern from the northern species of the genus.

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KEY TO LETTERING

- a.e. actinula exposed by rupture of gonophore wall.
- a.l. actinula larva.
- at. atriche.
- b. blastostyle.
- b.b. base of blastostyle.
- b.f.5. *a* blastostyle traced in fig. 5, *a*.
- b.f.5. *b* blastostyle traced in fig. 5, *b*.
- b.f.5. *c* blastostyle traced in fig. 5, *c*.
- b.l. base of long larval tentacle.
- b.t. blastostyle tentacle.
- b.y. blastostyles of the younger specimens lying close against those of the older specimen.
- c. capitulum of long larval tentacle.
- c.d. chitinoid disk.
- c.g. longitudinal ciliated groove.
- c.m. circular muscle process.
- c.t. endodermal cavity of tentacle.
- cn. cnidopods of atriches.
- cu. cuticle.
- d. desmoneme.
- d.t. degenerate short tentacles.
- e. egg membrane stretched round actinula larva.
- e.i. bases of terminal ectodermal cells inserted through mesogloea.
- e.l. endodermal lumen of spadix.
- e.me. attachment of egg membrane to spadix mesogloea.
- e.s. endodermal sphincter.
- e.t. connection between endoderm of tentacle and that of main body.
- e.v. vacuolate endodermal cell.
- e.y. young darkly staining endodermal cells.
- ec. exumbrella ectoderm.
- ect. ectoderm.
- ect.l. dendritic ectoderm of long larval tentacle.
- en. endoderm of bell of gonophore.
- en.s. endoderm of spadix.
- end. endoderm.
- end.l. endoderm of long larval tentacle.
- ex. exumbrella mesogloea.
- f. ciliated furrow between blastostyle villi which leads into spadix of gonophore.
- f.25. position of section shown in fig. 25, pl. III.
- g. stretched bell of gonophore.
- g.c. granules which will form chitinoid disk.
- g.e. sub-cuticular granules in ectoderm.
- g.s. shrunken gonophore wall.
- g.2-g.10 gonophores at successive stages of development situated on the blastostyle shown in fig. 15.
- g.10.s. gonophore at similar stage to that of g.10 in fig. 15, pl. II.
- gr. fuchsin staining granules.
- h. hydrorhiza adhesive tentacle.
- h.t. hydranth body tentacle.
- he. heteroneme.
- i.v. inner part of villus composed of darkly staining cells.
- j. junction of capitulum and stem.
- l. long larval tentacle.
- l.f. longitudinal mesogloea flanges projecting into ectoderm.
- l.h. endodermal lumen of adhesive tentacle.
- l.m. longitudinal muscles inserted on to mesogloea flanges, here cut transversely.
- l.mu. longitudinal muscle process.
- l.r. longitudinal endodermal ridge.
- l.t. capitulum and stem of long larval tentacle of actinula.

- m. mesogloea of spadix.
- m.b. mesogloea of blastostyle.
- m.b.t. mature blastostyle tentacle.
- m.f. apical pad of mesogloea fibrils.
- m.l. basal layer of solid mesogloea.
- m.o. outer part of mesogloea, insertions of enidopods causing the striated appearance.
- m.s. thickening of mesogloea supporting sphincter muscles.
- m.v. mesogloea of villus.
- m.w. mesogloea of body wall.
- me. mesogloea.
- n. nematocysts.
- n.n. nematocyst nursery.
- n.o. nucleus of oocyte recently fused with ovum and which has not yet degenerated.
- n.p. nerve plexus.
- n.s. darkly staining nutritive spheres.
- o. oocytes.
- ov. single ovum.
- ov.n. nucleus of single ovum.
- p. developing mesogloea fibrils.
- p.e. darkly staining peripheral layer of endoderm (embryonic cells).
- r. rudiment of gonophore endoderm.
- r.e. rudiment of ectodermal lining of gonophore.
- s. subumbrella mesogloea.
- s.b. connection between endodermal cavities of spadix and blastostyle.
- s.b.t. senile blastostyle tentacle.
- s.d. darkly staining disk of subumbrella ectoderm which will unite with exumbrella ectoderm to form a velar opening.
- s.e. subumbrella ectoderm.
- s.ec. spadix ectoderm lying outside oocytes.
- s.ex. union of ex- and subumbrella mesogloea (position of future velum).
- s.s. subumbrella space.
- s.t. small body tentacle.
- sp. spadix.
- sp.e. spadix ectoderm.
- st. stenotele.
- t.b. edge of tentacle base.
- t.f.4 position of parasagittal section shown in fig. 4.
- t.l. tentacle-bearing lobe of blastostyle.
- t.1. young developing tentacles.
- t.2. mature tentacles.
- t.3. degenerate tentacles.
- t.o. short tentacles covering oral pole of actinula.
- t.y. tentacle-bearing zone of young specimen lying close to the large specimen.
- v. rachis of *Virgularia* (substratum of hydroid).
- v.a. apex of rachis of *Virgularia*.
- v.c. binucleate vacuolate cell showing both nuclei.
- v.in. velar invagination.
- v.l. endodermal valve at base of long larval tentacle.
- vac. vacuole of endodermal vacuolate cell.
- vi. endodermal villus.
- x. point of union of spadix mesogloea "m." with the exumbrella "ex." and subumbrella "s." mesogloea lamellae.
- y.b.t. young blastostyle tentacle.
- y.g. young gonophore.
- y.h. young haploneme from nematocyst nursery.
- y.t. mature body tentacle at maximum size.
- z.y.b. zone of young blastostyles.

PLATE I: *M. PENOLA* and *M. CAPENSIS*

(Photographs by Dr. J. P. Harding)

FIG. 10.—Photograph of two specimens of the hydroid *Myriothele penola* attached to the apex of the rachis of the pennatulid *Virgularia*. The larger specimen is mature and measures 85 cm. Only the tentacle bearing zone of the smaller specimen (5.5 cm. long) can be seen, the blastostyles lie below those of the adult, and the hydrorhiza is attached to the same part of the *Virgularia*. $\times 0.48$.

FIG. 11.—Photograph of part of the blastostyle bearing zone of the mature specimen of *M. penola*, with the blastostyles pushed apart to show the body of the hydranth which is devoid of tentacles in this region. The blastostyle "b.f.5, a" is traced in fig. 5, a, p. 271, where the parts are labelled. This blastostyle bears an actinula larva retained only by the egg membrane, the gonophore wall having shrunk back. Four other gonophores bear actinulae of the same age, the tentacles of which can be seen through the transparent bell wall. Other gonophores present are much younger and smaller in size. $\times 1.7$.

FIG. 12.—*M. capensis*. Photograph is of an immature specimen which has been pulled off its substratum so as to expose the hydrorhiza. The chitinous disks of the hydrorhiza tentacles can be seen at "h." $\times 4$.

FIG. 13.—*M. capensis*. Photograph of an almost mature specimen attached to the brown alga *Echlonia radiata*. $\times 4.8$.

FIG. 14.—Photograph of the basal end of the mature specimen of *M. penola* showing the adhesive hydrorhiza tentacles fixed to the rachis of the pennatulid. Many hydrorhiza tentacles are unattached. Two blastostyles bearing hydrorhiza tentacles "b.f.5, b" and "b.f.5, c" are traced in figs. 5, b and 5, c, p. 271, so that the identification of the parts may be facilitated. The majority of the adhesive tentacles shown in the photograph arise directly from the hydranth body and not from the blastostyles. The uppermost part of the rachis of the *Virgularia* is obscured by the blastostyles of both individuals, and lies towards the bottom of the figure, the apex is at "v.a." $\times 1.7$.

BRITISH GRAHAM LAND EXPEDITION

Brit. Mus. (Nat. Hist.).

REPORT No. 4.

PLATE I

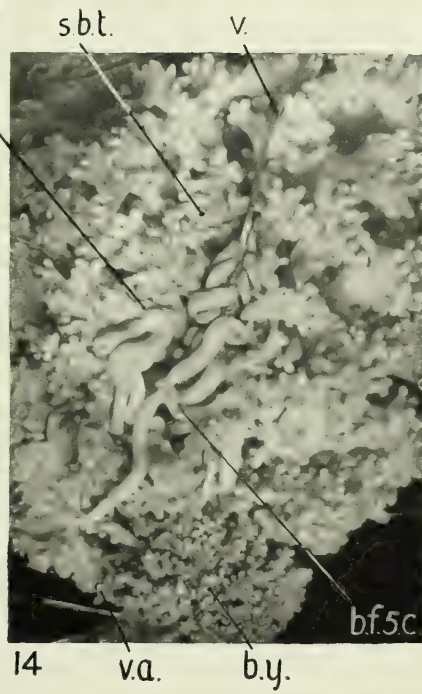
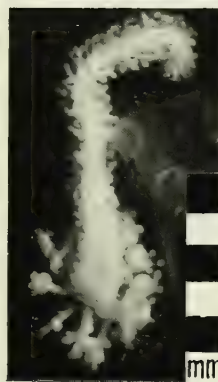
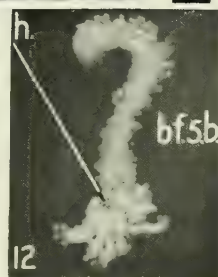
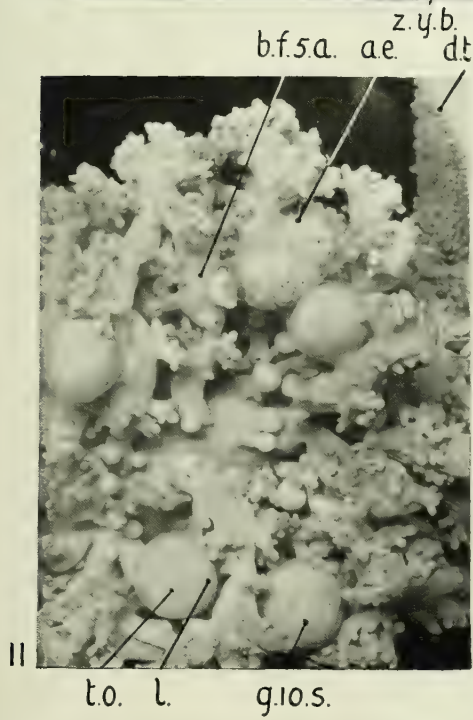
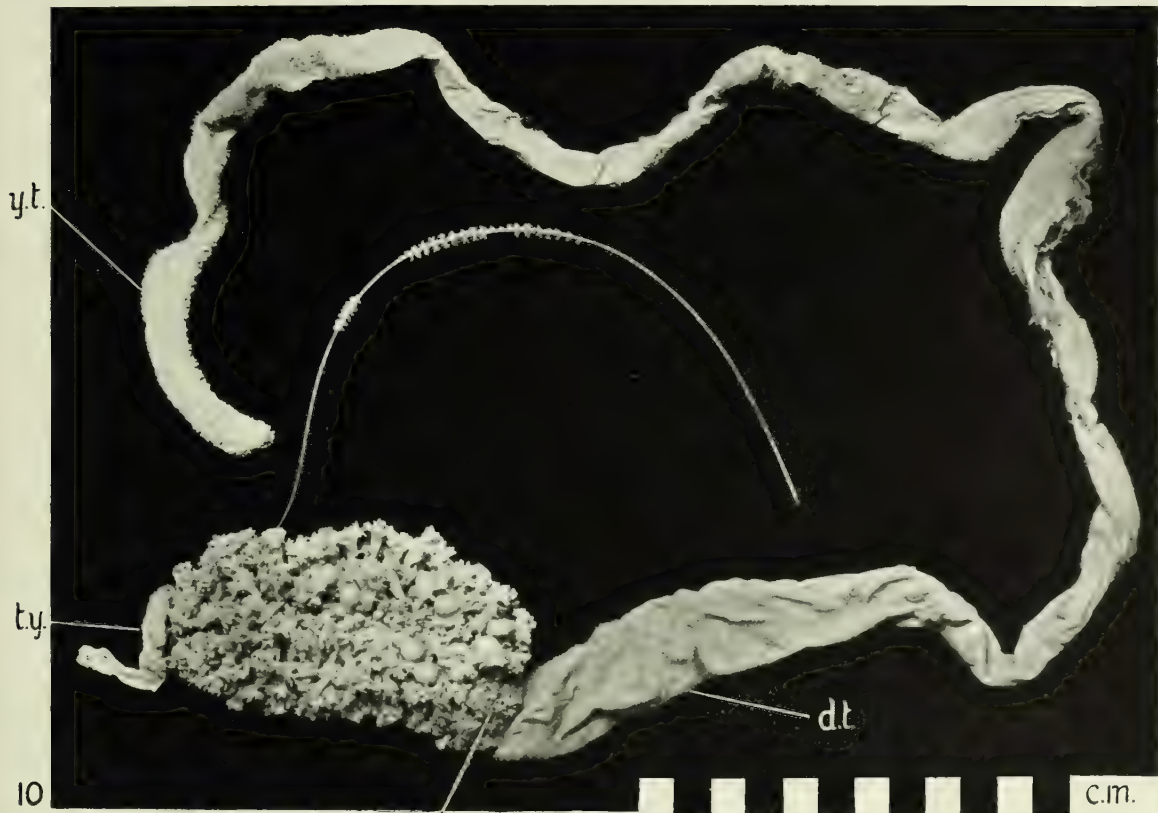


PLATE II: *M. PENOLA*

(Photographs of figs. 16—21 by Dr. A. F. W. Hughes and photographs of fig. 15 by Dr. J. P. Harding)

FIG. 15.—Photograph of a blastostyle from the mature female. The series of gonophores "g.1" to "g.10" are numbered in order of age. "g.10" contains an actinula ready for liberation, and "g.1", "g.3", and "g.6" are on the opposite side of the blastostyle. Tentacles "t.1", "t.2" and "t.3" are at progressive stages of development and degeneration. $\times 18$.

FIGS. 16–19 show blastostyle tentacles in sagittal section at progressive stages of development and degeneration. $\times 77$.

FIG. 16. Young tentacle ("t.1" fig. 15) and tentacle bearing lobe of blastostyle. Mesogloea fibrils "p" are just appearing and nematocysts are few.

FIG. 17.—Mature tentacle ("t.2", fig. 15) with fully formed pad of mesogloea fibrils "m.f." and differentiated endoderm.

FIG. 18.—Older tentacle with shorter mesogloea fibrils, and many more granules in the lateral endoderm.

FIG. 19.—Degenerate tentacle ("t.3" fig. 15), the capitulum has merged into the stem, mesogloea fibrils and nematocysts are absent, and the undifferentiated endoderm is charged with granules.

FIG. 20.—Sagittal section of female gonophore "g.9", fig. 15. The exumbrella mesogloea is of considerable thickness "ex.", and within it can be seen the bell endoderm, but the subumbrella mesogloea and ectoderm are almost invisible at this magnification (see text-fig. 4). The dark inclusions in the endodermal villi are nutritive spheres "n.s.", and the clear dots in the villi are the vacuoles "vac." of the vacuolate cells. $\times 40$.

FIG. 21.—Sagittal section of the female gonophore "g.10" fig. 15. The spadix has shrunk "sp.", and the actinula is now occupying the subumbrella space. The two layers of bell mesogloea "s." and "ex." and the spadix mesogloea "m." are clearly seen, and the latter adheres to the egg membrane "e." The aboral pole of the larva lies towards the spadix and is covered by adhesive hydrorhiza tentacles "h."; the rest of the larva is clothed with small tentacles "s.t.", and the long larval tentacles "l." which are folded round the body. The oral pole of the larva is not cut in this section. $\times 22$.

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PLATE II

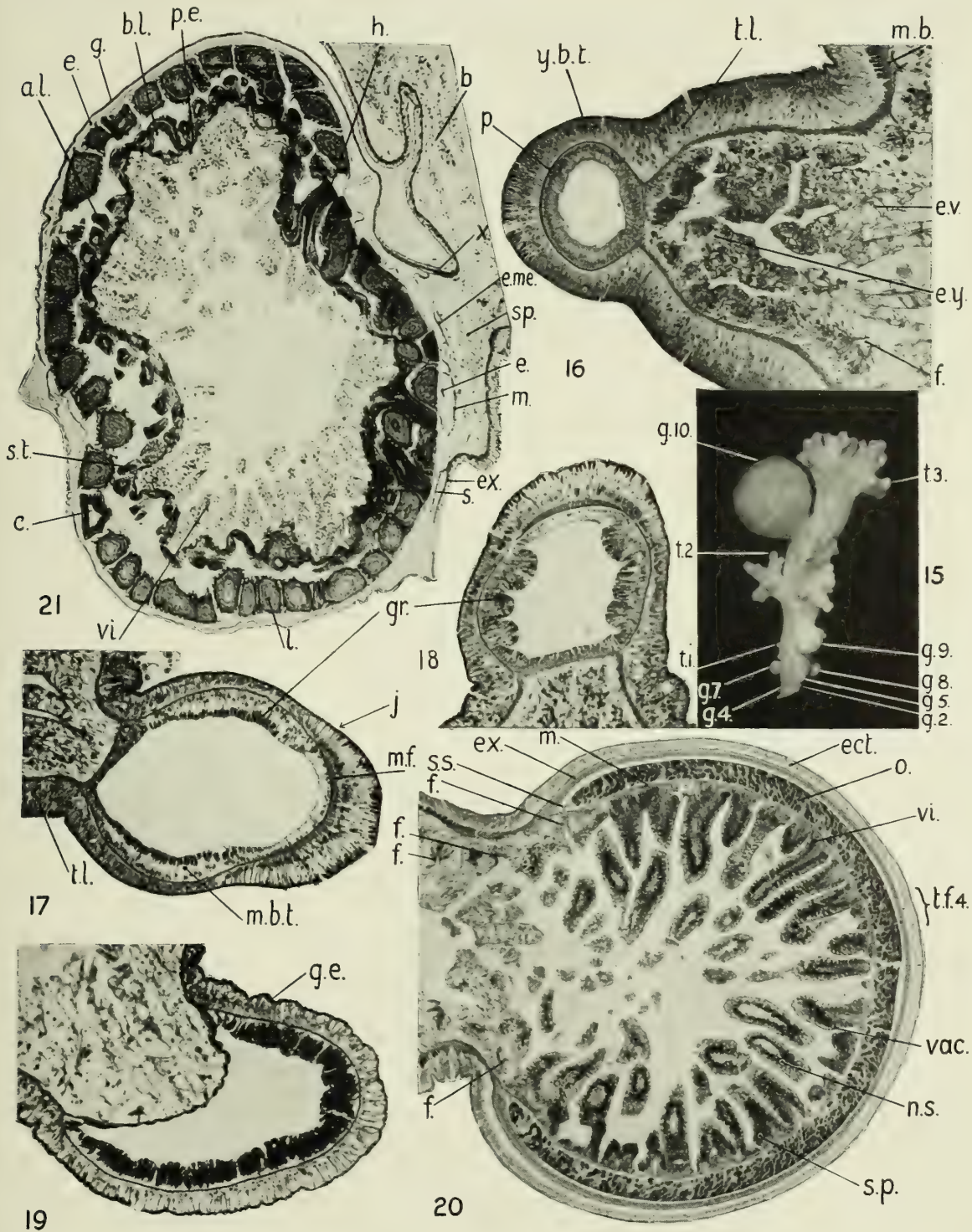


PLATE III: *M. CAPENSIS* and *M. PENOLA*

(Photographs of figs. 22—24 by Dr. I. Manton; photographs of figs. 25—28 by Dr. A. F. W. Hughes.)

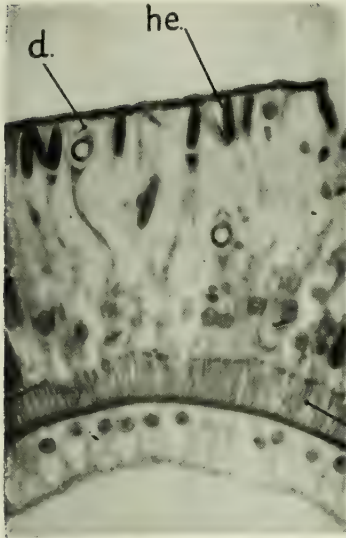
- FIG. 22.—Sagittal section through the apex of the capitulum of a blastostyle tentacle of *M. penola* showing the superficial layer of heteronemes and two desmonemes. The cnidopod of the desmoneme "d." near the surface is straight (the proximal part of the cnidopod is not in the same plane), compare fig. 23. $\times 385$.
- FIG. 23.—Similar section to fig. 22, showing a desmoneme in the deeper part of the ectoderm with its coiled cnidopod. $\times 770$.
- FIG. 24.—Sagittal section through the capitulum of a long larval tentacle from the actinula of *M. penola* showing details of the nematocysts, $\times 770$; compare with the smaller magnification shown in fig. 29, pl. IV.
- FIG. 25.—Part of sagittal section of a mature body tentacle of *M. penola*, the position of this region is shown in text-fig. 2 "f.25". The capitulum nematocysts are seen at the side of the apical pad of mesogloea fibrils. The endodermal circular muscle processes "c.m." lie against the right-hand side of the mesogloea; below lies the mesogloea support of the sphincter at the base of the capitulum. $\times 280$.
- FIG. 26.—Transverse section through the wall of the basal part of a mature blastostyle of *M. penola*. Close-set villi are separated by ciliated grooves, and the binucleate nature of the vacuolate cells is clearly seen. $\times 77$.
- FIGS. 27 and 28.— Transverse sections of the body wall of *M. capensis* and *M. penola* respectively to show the difference in the proportions of the parts of the mesogloea.
- FIG. 27.—Body wall of *M. capensis* from the middle of the tentacular region. $\times 280$.
- FIG. 28.—Body wall of *M. penola* from the upper third of the tentacular region. $\times 264$.

BRITISH GRAHAM LAND EXPEDITION

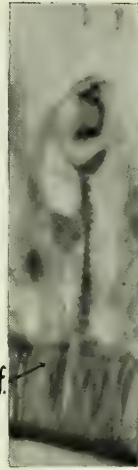
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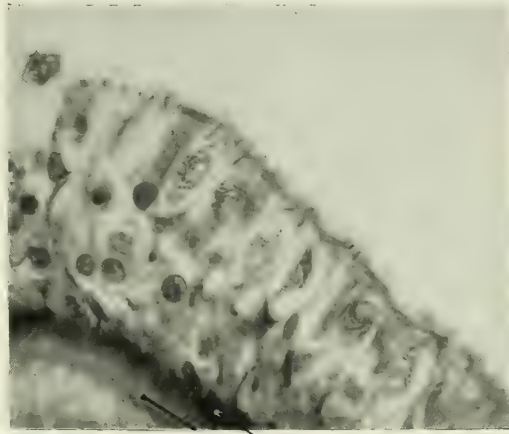
PLATE III



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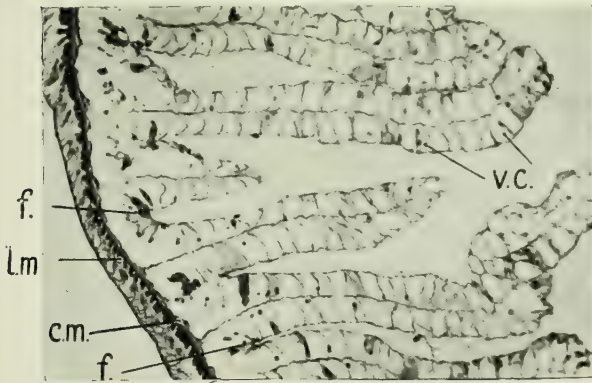


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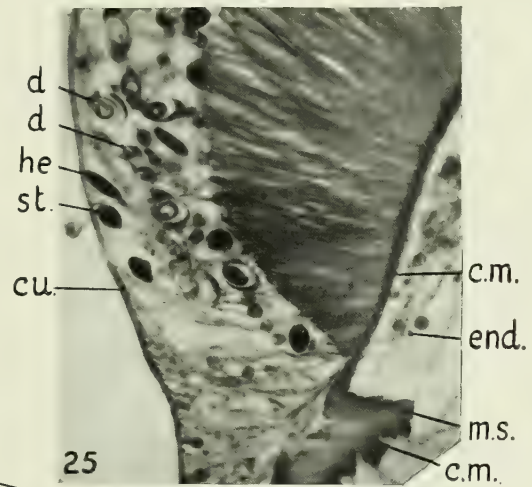


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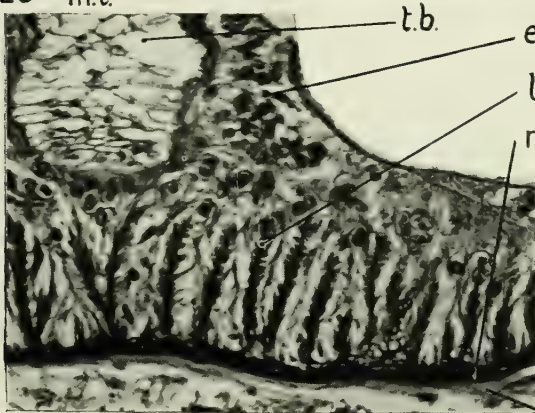
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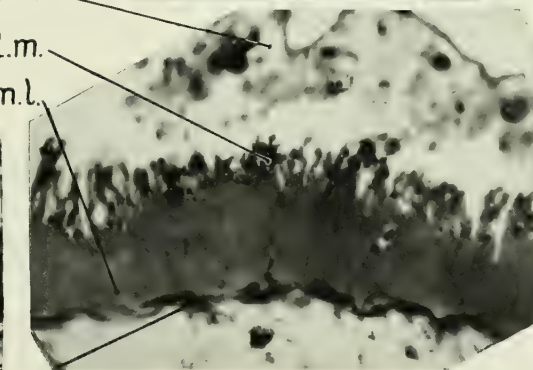
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25



27



c.m. 28

PLATE IV: *M. PENOLA*

(Photographs by Dr. A. F. W. Hughes.)

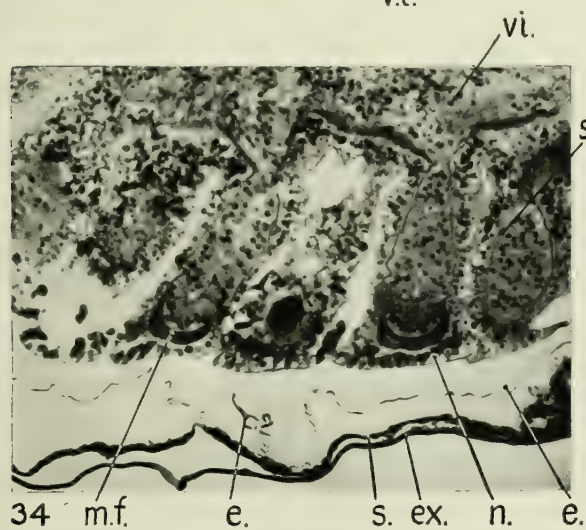
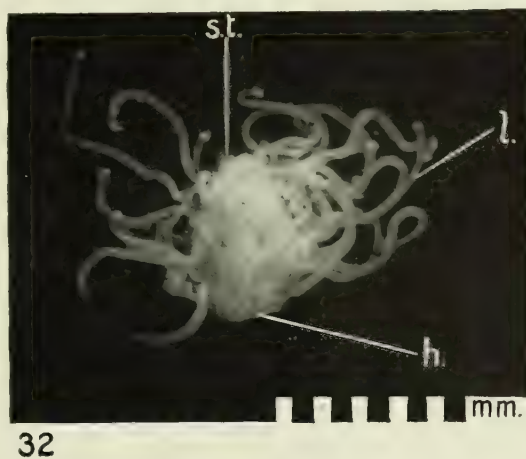
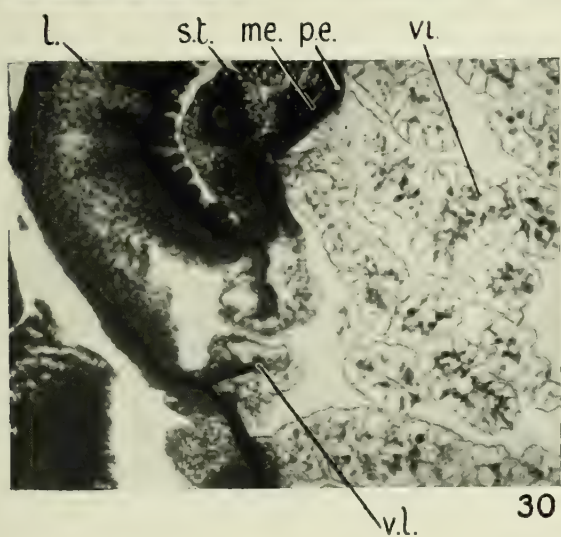
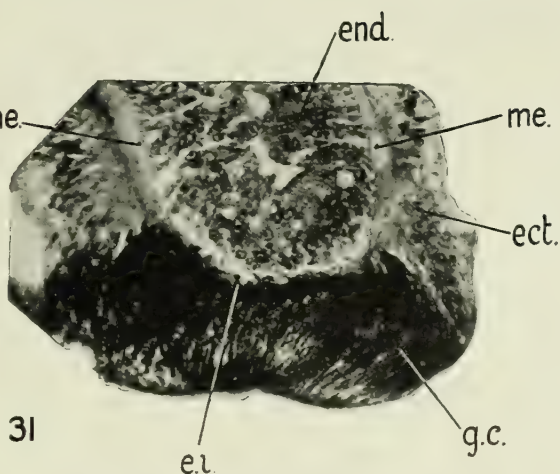
- FIG. 29.—Sagittal section through the capitulum of a long larval tentacle of the actinula. The cnidopods "c.n." of the atriches are inserted into the outer layer of mesogloea, for details of the capsules see fig. 24, pl. III, and for stem of the tentacle see fig. 33. $\times 300$.
- FIG. 30.—Section of the actinula body wall passing through the base of a long larval tentacle and showing the endodermal valve situated in this position. The limits of the mesogloea, so clear in a Mallory stained preparation, have been touched up on the photograph, as there is such a small difference in intensity between the reds and the blue colour. The dark spots in the villi are nutritive spheres and endodermal nuclei. $\times 80$.
- FIG. 31. Sagittal section through the tip of an adhesive hydrorhiza tentacle from the actinula. For the appearance of the whole tentacle at a smaller magnification, see fig. 21, pl. II, "h." The bases of the terminal ectoderm cells, which are laden with fuchsin-staining granules (black), are seen to be inserted into and through the mesogloea layer. These granules will later form the chitinous disk. $\times 220$.
- FIG. 32.—Actinula larva removed from gonophore just before its liberation. The long larval tentacles have been uncoiled to expose the body. $\times 2.5$.
- FIG. 33.—Section through the middle region of the actinula showing the short body tentacles in sagittal section, and the stem of a long larval tentacle lying outside these and cut in longitudinal section (for capitulum, see fig. 29). $\times 80$.
- FIG. 34.—Section through the oral pole of the actinula showing the short body tentacles which are here not covered by the long larval tentacles. The villi are here so close together that there is no room for the peripheral endodermal layer of darkly staining cells; compare figs. 33 and 21. The gonophore wall and the stretched egg membrane are seen outside the tentacles. $\times 135$.

BRITISH GRAHAM LAND EXPEDITION

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REPORT No. 4.

PLATE IV



BRITISH MUSEUM (NATURAL HISTORY)

BRITISH GRAHAM LAND EXPEDITION

1934-37

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ANOPLURA

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WITH ONE PLATE AND ELEVEN TEXT FIGURES

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ANOPLURA

By THERESA CLAY, B.Sc.

Department of Entomology, British Museum (Natural History)

THE collection of Anoplura presented to the British Museum by the British Graham Land Expedition was collected by Mr. Brian Roberts and comprises some interesting material. The collection contains two species of Siphunculata (sucking lice) and 17 species of Mallophaga (biting lice), of which two are certainly new and two others are possibly new but cannot be described until further material is available. The most interesting species in the collection are *Antarctophthirus lobodontis* Enderlein, a little known species; the species of *Tetrophthalmus*, a genus which is found in the pouch of pelicans and cormorants and which has been only rarely recorded from these latter hosts; and the two new species of *Naubates* which together with *N. annu-liventrīs* form a distinct and interesting group within this genus.

As is usual when working out any collection of Mallophaga it is necessary to do a considerable amount of work on the characters and synonymy of related species, and in the cases where this has been done the results have been incorporated in the paper.

Owing to the inadequacy of the descriptions and figures of the majority of species of Mallophaga it is necessary to have specimens from the type hosts for identification; also, in order to get a true conception of the genera comprising the species from a single order of birds, material from as many hosts as possible within that order is needed. The author is fortunate therefore in being able to work on Colonel Meinertzhagen's large and unique collection without which the correct identification of this material would have been difficult. The author is also indebted to Dr. Delkeskamp of the Berlin University Zoological Museum for the loan of Enderlein's types; to Professor Martin of the National Veterinary School of Toulouse for the loan of Neumann's types; to Mr. G. H. E. Hopkins for valuable advice; and to Dr. E. A. Chapin for information concerning the type of *Tetrophthalmus transitans* and for the great assistance afforded to the author while in the National Museum at Washington.

Text-figures 1, 7*b* and 10 were drawn by Miss Mackay, the remainder by the author.

Order ANOPLURA

Sub-order SIPHUNCULATA

Genus *Antarctophthirus* Enderlein*Antarctophthirus lobodontis* Enderlein 1907.

1 ♂, 1 ♀, 13 immature collected from hind limbs of an immature diseased specimen of *Lobodon carcinophagus* (Jacquinot and Pucheran). Argentine Island, W. Graham Land.

These specimens have the ventral hairs on the mid-thoracic region as shown in Enderlein's original figure and are distinguished from *microchir* and *callorhini*, which also possess this character, by the absence of hairs on the mid-dorsal region of thorax and abdomen.

Antarctophthirus sp.?

4 ♂, 31 ♀, 1 immature from young *Leptonychotes weddelli* (Lesson). Argentine Island, W. Graham Land.

These specimens are apparently conspecific with *A. ogmorhini* Enderlein, but the poor condition of the types of the latter makes an exact determination impossible.

Sub-order MALLOPHAGA

Super-family AMBLYCERA

Family MENOPONIDAE

Genus *Menopon* Nitzsch*Menopon becki* Kellogg 1906.

2 ♀ from under wing of *Phaethon a. aethereus* Linné. N.E. of Cape Verde Islands.

These specimens are apparently conspecific with the species figured by Thompson (1938) as *M. becki*. However, as the original description of this species was unaccompanied by a figure it cannot be said with certainty that these specimens are *M. becki* until the type has been examined.

Genus *Tetrophthalmus* Grosse*Tetrophthalmus* sp.?

82 ♂, 61 ♀, 41 immature from 5 adults and an unspecified number of newly-hatched chicks of *Phalacrocorax a. atriceps* King, from the Bethelot, Uruguay, and Argentine Islands, and Port Lockroy, Graham Land. These specimens were collected inside the mouth and in the case of one adult and some of the newly-hatched chicks from the head skin. One immature bird had 154 specimens of this parasite inside the mouth.

2 ♂ from inside the mouth of *Phalacrocorax a. albiventer* (Lesson), from Kidney Island, E. Falkland.

Records of *Tetrophthalmus* from cormorants are rare so that these specimens from new hosts are of considerable interest. *Tetrophthalmus* on cormorants was first recorded by Kellogg and Chapman (*T. incompositus*, 1899, p. 123) from *Phalacrocorax penicillatus* (Brand), although the authors themselves expressed some doubt as to the authenticity of the host and suggested that the single specimen, on which the description was based, might have straggled from a pelican. However, the description and figure¹ show without doubt that *incompositus* is a cormorant parasite. Ewing (1930, p. 125), described *T. transitans* from a single male specimen taken from an unknown cormorant found in the stomach of a gull from Chincha Island, Peru. Specimens of *Tetrophthalmus* recently sent to the British Museum from *Phalacrocorax bougainvilli* (Lesson), collected at Pisco, Peru, appear to be *transitans* when compared with drawings of the type made by the author while in Washington. *Phalacrocorax bougainvilli* should therefore be considered as the type host of *T. transitans* Ewing. *Tetrophthalmus* has also been recorded from *Phalacrocorax a. auritus* (Lesson) by Peters (1928, p. 222), and Lewis (1929, p. 81).

Through the kindness of Professor F. H. Wilson of the Tulane University the author has been able to examine *Tetrophthalmus* from *Phalacrocorax auritus* and, together with the material mentioned above, has now seen specimens from all the hosts from which *Tetrophthalmus* has been recorded with the exception of *Phalacrocorax penicillatus*. This is unfortunate as without material from this host, the type host of *incompositus*, identification of the other material is not possible. As soon as material from *P. penicillatus* is available it is hoped to publish descriptions of all the known cormorant *Tetrophthalmus*, but until then the identification of the *Tetrophthalmus* collected on the British Graham Land Expedition must be left uncertain.

Super-family ISCHNOCERA

Family PHILOPTERIDAE

Genus *Austrogoniodes* Harrison

? *Austrogoniodes hamiltoni* Harrison 1937.

Austrogoniodes hamiltoni Harrison, 1937, p. 18, pl. i, f. 8-9, pl. ii, f. 1-2. Type host: *Eudyptes c. cristatus* (Miller). (Corrected from *Catarrhactes pachyrhynchus* on p. 6.)

1 ♂, 1 ♀, 8 immature, from *Eudyptes c. cristatus* (Miller). Kidney Island, E. Falklands.

These specimens appear identical with paratypes of *A. hamiltoni* in the British Museum, except that in the case of the single male collected on this Expedition the genitalia are proportionally somewhat smaller.

Genus *Philopterus* (sens. lat.)

? *Philopterus bicolor* (Rudow) 1870.

1 ♂ from *Priocella antarctica* (Stephens), Clarence Island, S. Shetlands.

¹ The figure shows a female, not a male as stated in the text.

Philopterus spp. ?

1 ♂ from *Daption capensis* (Linné), Clarence Island, S. Shetlands.

1 ♀ from *Daption capensis*, Leith, S. Georgia. Apparently a different species from the male.

As it has been impossible to examine specimens of *Philopterus* from all the type hosts of the species occurring on the Procellariiformes it has been considered advisable to leave the exact determinations of these three species until more material is available.

? *Philopterus platycephalus* (Kellogg and Kuwana) 1902.

3 ♂ from *Garrodia nereis* (Gould), Kidney Island, E. Falklands.

It is not possible to say from the description and figure whether these specimens from *Garrodia nereis* are conspecific with *P. platycephalus* from *Oceanites gracilis galapagoensis* Lowe. However, it is apparent that they are closely related if not conspecific but must await the examination of material from the type host of *platycephalus* before being identified with certainty.

Docophoroides Giglioli*Docophoroides brevis* (Dufour), 1835.

11 ♂, 8 ♀, 21 immature, collected from the head and neck of 4 adult *Diomedea exulans* Linné. At sea, latitude 56° 20' S., longitude 61° 18' W.

Docophoroides harrisoni Waterston 1917.

1 immature from neck of *Diomedea m. melanophris* Temminck. At sea, latitude 60° 24' S., longitude 62° 55' W.

The specimen is somewhat immature but should probably be referred to this species.

Family ESTHIPTERINAE

Genus *Pseudonirmus* Mjöberg*Pseudonirmis gurlti* (Taschenburg), 1882.

5 ♂, 11 ♀ collected from 4 specimens of *Daption capensis* (Linné). Deception Island, S. Shetlands, and S. Georgia.

Genus *Episbates* Harrison*Episbates pederiformis* (Dufour), 1835.

2 ♂, 2 ♀ from *Diomedea exulans* Linné. At sea, latitude 56° 20' S., longitude 61° 18' W.

? *Harrisionella ferox* (Giebel) 1867.

Lipeurus ferox Giebel, 1867, p. 195. Type host: *Diomedea m. melanophris* Temminck.

1 ♂, 1 ♀ from underside of primary wing feathers of *Diomedea exulans* Linné. At sea, latitude 56° 20' S., longitude 61° 18' W.

As is shown below it is not possible to use *diomedae* Fabricius for the species placed in *Harrisonella* by Bedford nor can *diomedae* Dufour be used, as it is merely a mis-identification of the species of Fabricius. *L. ferox* was described from *Diomedea melanophris* and as material has not been examined from this host it is impossible to determine the specimens from *D. exulans* with certainty.

Genus *Perineus* Harrison

Perineus nigrolimbatus (Giebel) 1874.

1 ♂, 6 ♀ from under wing of 2 specimens of *Priocella antarctica* (Stephens) from Clarence Island, S. Shetlands.

Specimens of this type of *Perineus* have been examined from *Fulmarus glacialis* (type host of *nigrolimbatus*), *Priocella antarctica* and *Daption capensis*. There is a certain amount of variation in the characters of these specimens especially at the point of approximation of the frontal bands in the mid-line of the head, but as any given type of variation is not restricted to the specimens from one host it cannot be considered of specific value. The head index, i.e., the proportions of breadth to length of the whole head and the breadth to length of the pre-antennal region show that on an average specimens from *Fulmarus glacialis* have a smaller and narrower head than either those from *Daption* or *Priocella*. However, a much larger number of specimens will have to be measured before any conclusions can be reached. If, on the examination of a large amount of material it is found that the specimens from the different hosts are separable, it must be remembered that the single female type specimen of *mutabilis* Piaget in the British Museum, labelled as from *Procellaria glacialis* (= *Fulmaris glacialis*) falls well within the range of the large specimens from *Priocella* and has a broader head than any of the specimens measured from *Fulmarus*. It is possible, therefore, that Piaget was mistaken as to the host, a suggestion which is borne out by the fact that amongst the old material in the Leiden Museum, which was most probably examined by Piaget, is a specimen of *Priocella antarctica* labelled *P. glacialis*.

Specimens from *Priocella antarctica* are therefore placed temporarily in *nigrolimbatus*, although eventually they may prove to be subspecifically separate.

The genus *Perineus* contains a number of rather diverse species amongst which there is a group of related species, all of which exhibit great contrast between the pigmented and non-pigmented areas. As it has been possible to examine specimens of all the known species of this group with the exception of one, and as it has been necessary to go into the characters and synonymy of them all in order to name the species collected on this Expedition, it has been thought advisable to include a short account of these species and their synonymy.

Perineus diomedae (Fabricius) 1775. (Text-figs. 1, 2, 4a, 5a and 6a.)

Pediculus diomedae Fabricius, 1775, p. 808. Original host record: "In Brasiliae diomedeis". Type host (by present designation): *Diomedea m. melanophris* Temminck.

Lipeurus meridionalis Rudow, 1869, p. 32. Type host: *Phoebetria p. palpebrata* (Forster) (*Diomedea fuliginosa*).

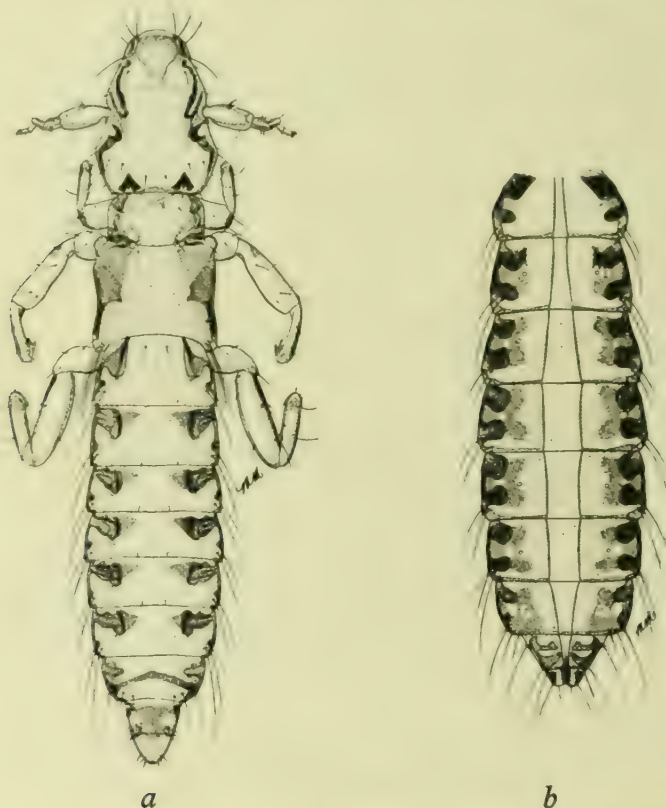
Lipeurus tricolor Piaget, 1880, p. 363, pl. XXX, f. 4. Type host: *Phoebetria p. palpebrata* (*Diomedea fuliginosa*).

Lipeurus lepturus Enderlein, 1909, p. 452, pl. LXII, f. 200-2, 209. Type host: *Phoebetria p. palpebrata* (*Diomedea fuliginosa*).

Esthiopterum ferreirai Monteiro de Barros, 1933, p. 33, 3 pls. Type host: *Diomedea m. melanophrys* Temminck (*Diomedea melanophrys*).

2 ♂, 1 ♀ collected from secondary wing feathers of *Diomedea m. melanophrys* Temminck. At sea, latitude 60° 24' S., longitude 62° 55' W.

Mr. G. H. E. Hopkins, in a private communication to the author, has pointed out that the description of *diomedae* Fabricius cannot be interpreted to represent a species of *Harrisonella*. Mr. Hopkins says: "The description is quite certainly that

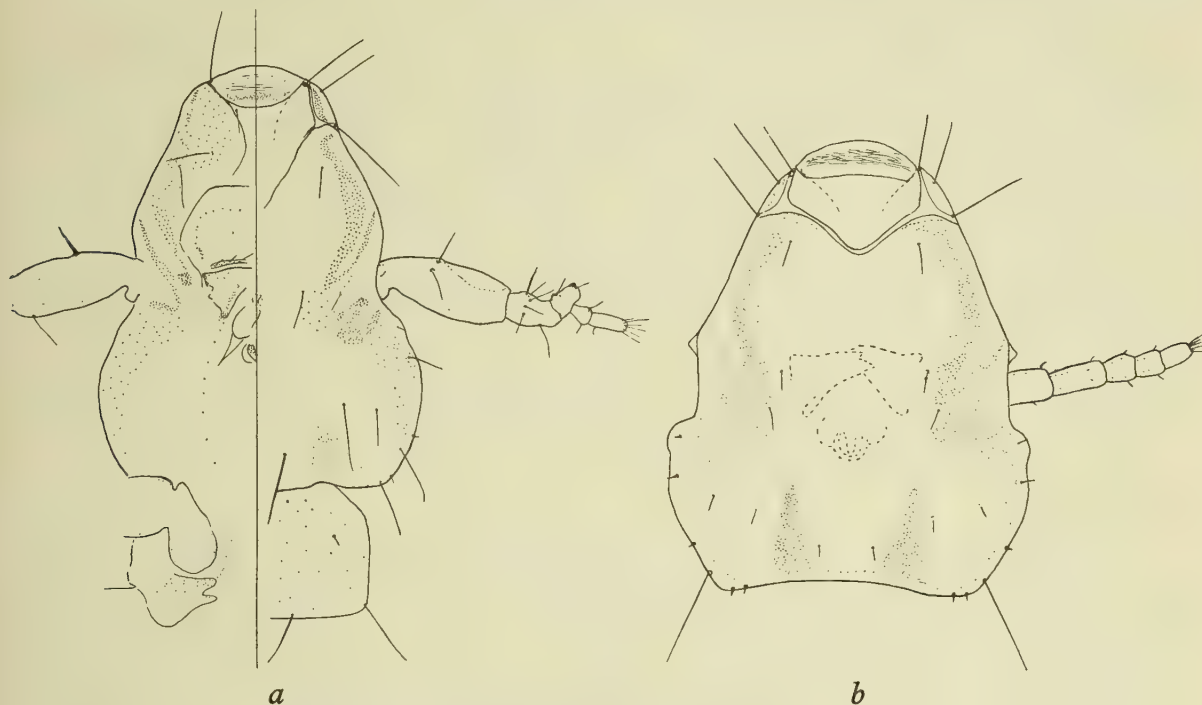


TEXT-FIG. 1.—*Perineus diomedae*. (a) ♂; (b) ♀ abdomen.

of an *Esthiopterum* s.l. and the host-record is 'Habitat in Brasiliae diomedeis'. Harrison (1916, p. 13) referred the species to *Esthiopterum*, with *Lipeurus ferox* Giebel as a synonym, presumably because Taschenberg (1882, p. 145) placed *Pediculus diomedae* Fabricius as a synonym of *L. ferox*, in which he was followed by Kellogg. But this attribution is certainly erroneous and is probably due to confusion between *Philopterus diomedae* Dufour (which is the same as *ferox*) and *Pediculus diomedae* Fabricius. Fabricius' description informs us that the species is white with broad black abdominal margins and with white legs, which is wholly at variance with *ferox*, of which the adults are very dark-coloured and even immature forms have the legs mainly dark brown. Furthermore, *ferox* is a distinctly uncommon species, so that the probabilities would be against Fabricius' species being this even if there were not such grave discrepancies in the description. On the other hand the genus *Perineus*,

which is common on albatrosses, agrees almost perfectly with the description, even to the white legs, and I have no hesitation in ascribing *Pediculus diomedae* F. to this genus." Mr. Hopkins goes on to say that on *Diomedea m. melanophris*, one of the commoner albatrosses of Brazilian waters, there is a *Perineus* which fits excellently the description given by Fabricius. The present author has therefore designated and described below a neotype from *Diomedea m. melanophris*.

Although Rudow's original description of *meridionalis* does not give much indication as to what this species represents, Taschenberg (1882, p. 194) who apparently



TEXT-FIG. 2.—*Perineus diomedae*. Heads. (a) ♂; (b) ♀.

saw an immature example of Rudow's material, considered it to be conspecific with *tricolor* Piaget. The types of *tricolor* and *lepturus* and paratypes of *ferreirai* have been examined and in addition a considerable amount of material from *Diomedea melanophris* and *Phoebetria* spp. It is apparent from this material that specimens from *Diomedea melanophris* cannot be separated from those from *Phoebetria* for, although there is considerable variation in the amount and shape of the pigmented areas, this variation is found in specimens from both hosts.

This species is distinguished from those below by the smaller size, proportions of head, characters of male genitalia, and genital region of female.

Male.—Head with characters as shown in text-fig. 2a,

Thorax as shown in text-fig. 1a, with breadth of prothorax not greater than length of occipital margin of head. Sternal plates may either be completely pigmented, partially pigmented anteriorly, or apparently absent. Dorsal chaetotaxy as in figure; ventral surface with one mesothoracic hair each side.

Abdomen as shown in text-fig. 1a, with segments VIII and IX considerably narrowed. On the dorsal surface segment I has two anterior and two posterior

central hairs and two lateral hairs each side; segments I–VI with two small central hairs and two lateral hairs each side; segment VII with four hairs. On the ventral surface segments I–V with one lateral and two minute central hairs; segment VI with one lateral and four central hairs. Chaetotaxy of posterior segments as shown in text-fig. 4a.

Genitalia are quite distinct from those of *confidens* and *miriceps* in the narrow thickened paramera and from *hyalinus* in size and shape. Total length of genital apparatus figured in text-fig. 5a is 0.80 mm.

Female.—Head as shown in text-fig. 2b.

Thorax as in male.

Abdomen as shown in text-fig. 1b, with postero-lateral angles of segment VII not drawn out posteriorly. Vulva and chaetotaxy of genital region as shown in text-fig. 6a. Chaetotaxy of segments I–VI as in male.

MATERIAL EXAMINED: *Lectotype* of *tricolor* (Piaget) designated by present author; ♂ in the Piaget collection, slide No. 451. *Paratype*: 1 ♀.

Lectotype of *lepturus* (Enderlein) designated by present author; ♂ in the Berlin University Zoological Museum, from *Phoebetria p. palpebrata* from Prince Edward Island. *Paratypes*: 3 ♀.

In the material kindly lent by the Berlin Museum are 1 ♂, 2 ♀ (presumably those mentioned by Enderlein 1909, p. 453), from *Diomedea exulans* labelled *tricolor* by Enderlein; these specimens are conspecific with *lepturus*.

Paratypes of *ferreirai* (Monteiro de Barros): 1 ♂, 1 ♀ in the Meinertzhagen Collection.

22 ♂, 32 ♀ from skins and fresh specimens of *Diomedea m. melanophris* Temminck from Brazil, Valparaiso, and S. Georgia; 8 ♂, 16 ♀ from skins of *Phoebetria p. palpebrata* from the Antipodes Island and Kerguelen; 5 ♂, 7 ♀ from skins of *Phoebetria f. fusca* (Hilsenberg) from S. Atlantic.

Neotype of *diomedae* (Fabricius) designated by the present author; ♂ in the British Museum (presented by Mr. G. H. E. Hopkins), slide No. 309, from *Diomedea m. melanophris* Temminck from S. Paulo, Brazil. *Neoparatypes*: 21 ♂, 32 ♀ in the British Museum, Hopkins and Meinertzhagen Collections, from the same host from different localities.

Perineus confidens (Kellogg), 1899. (Text-figs. 3a, 4c & 5b)

Lipeurus confidens Kellogg, 1899, p. 26, pl. iii, f. 1. Type host: *Diomedea nigripes* Audubon.

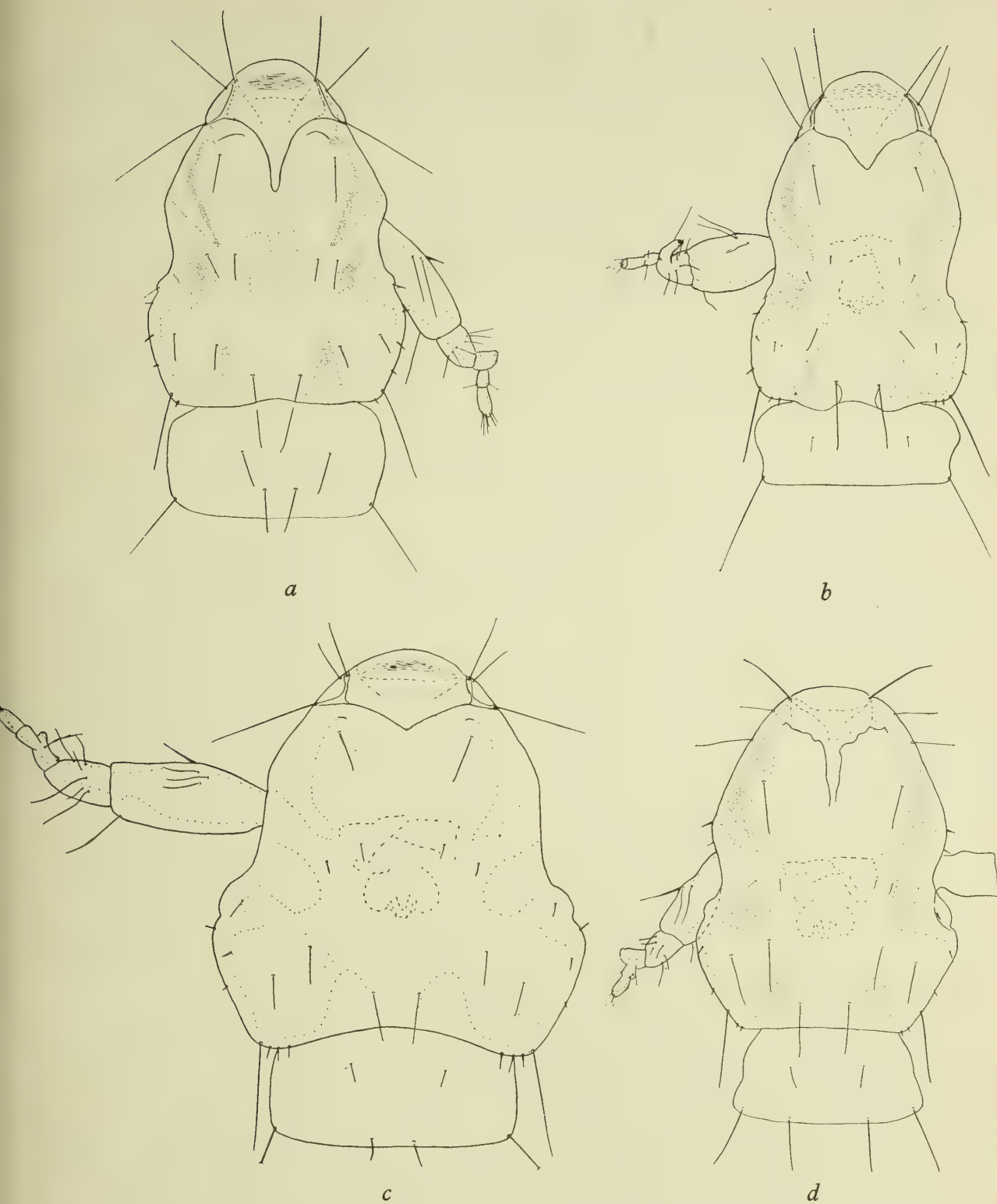
This species is distinguished from *diomedae* by its larger size and different proportions of head and from *miriceps* by the greater width of temples.

Male.—Head as shown in text-fig. 3a.

Prothorax with breadth equal to length of occipital margin of head. Pterothorax with general characters and chaetotaxy as in *diomedae*.

Abdomen with general characters as in *diomedae*, but with postero-lateral angles of segment VII produced posteriorly and posterior margin of last segment asymmetrical (text-fig. 4c). Chaetotaxy as in *diomedae*, but lateral dorsal hairs tend to be longer and stouter.

Genitalia are but slightly thickened and are therefore apt to become somewhat



TEXT-FIG. 3.—*Perineus* spp. ♂ heads. (a) *P. confidens*; (b) *P. miriceps*; (c) *P. hyalinus*; (d) *P. obscurus*.

distorted in mounting. Paramera differ from those of *diomedeae* in being flattened and unthickened (text-fig. 5*b*). Total length of genital apparatus is 1.23 mm.

Female.—Head with characters similar to that of *diomedeae* but with different measurements, and lacks lateral pigmented area running from ocular blotch to middle of temples.

Thorax as in male.

Abdomen similar in general character to *diomedeae* but with postero-lateral angles of segment VII produced somewhat posteriorly. Vulva and chaetotaxy of genital region apparently identical with that of *miriceps* although the breadth of the segments is greater. Chaetotaxy as in *diomedeae* except that segment I has four central hairs on the ventral surface and the lateral dorsal hairs tend to be longer and stouter in all segments.

MATERIAL EXAMINED: 5 ♂, 7 ♀ from skins of *Diomedea nigripes* Audubon from N. Pacific. 18 ♂, 18 ♀ from skins of *Diomedea irrorata* Salvin from Galapagos Islands.

Perineus miriceps (Kellogg and Kuwana) 1902. (Text-figs. 3*b*, 5*c* and 6*b*)

Lipeurus miriceps Kellogg and Kuwana, 1902, p. 480, pl. XXX, f. 4. Type host: *Geospiza fuliginosa* Gould (in error).

The host as given by Kellogg and Kuwana is a finch, and obviously not the true host of this species. This type of *Perineus* appears to be restricted to the genera, *Diomedea*, *Macronectes* and *Phoebastria*, and as the only species of these genera occurring in the Galapagos Islands (the locality of the species) is *Diomedea irrorata* Salvin, it should, as suggested by Thompson (1938¹, p. 490) be considered as the type host. Thompson, without stating his reasons, places this species as a synonym of *confidens* (Kellogg), but if the present interpretation of *miriceps* is correct the two species are quite distinct. Material examined from *D. irrorata* appears identical with the figure and description of *miriceps* except for the text measurement of the breadth of the head, this latter measurement being considerably smaller than that of any known species of *Perineus*. If the head index is calculated from the text measurements the result (i.e. C.I. = 0.36) is different from that calculated from the measurements taken from the figure (i.e. C.I. = 0.62). However, if it is assumed that the text measurement of the breadth of the head, i.e. 0.31 mm. is a mistake for 0.51 mm., the head index (i.e. 0.60) is then within the range of those taken from the figure and from specimens from *D. irrorata* (i.e. 0.62–0.66). There seems to be little doubt therefore that 0.31 mm. for the breadth of the head is an error.

This species is distinguished from *confidens* by the proportions of the head in both sexes, by the narrow temples and the male genitalia.

Male.—Head as shown in text-fig. 3*b*.

Thorax normal but with prothorax somewhat enlarged antero-laterally.

Abdomen with general characters as in *diomedeae* but with postero-lateral angles of segment VII drawn out posteriorly to a greater extent and with posterior margin of last segment asymmetrical. Chaetotaxy of abdomen as in *confidens*.

Genitalia similar in general characters to those of *confidens* but differing in detail (text-fig. 5*c*). Total length of genital apparatus is 1.18 mm.

Female.—Head similar to that of *confidens* but differing in proportions.

Thorax as in male.

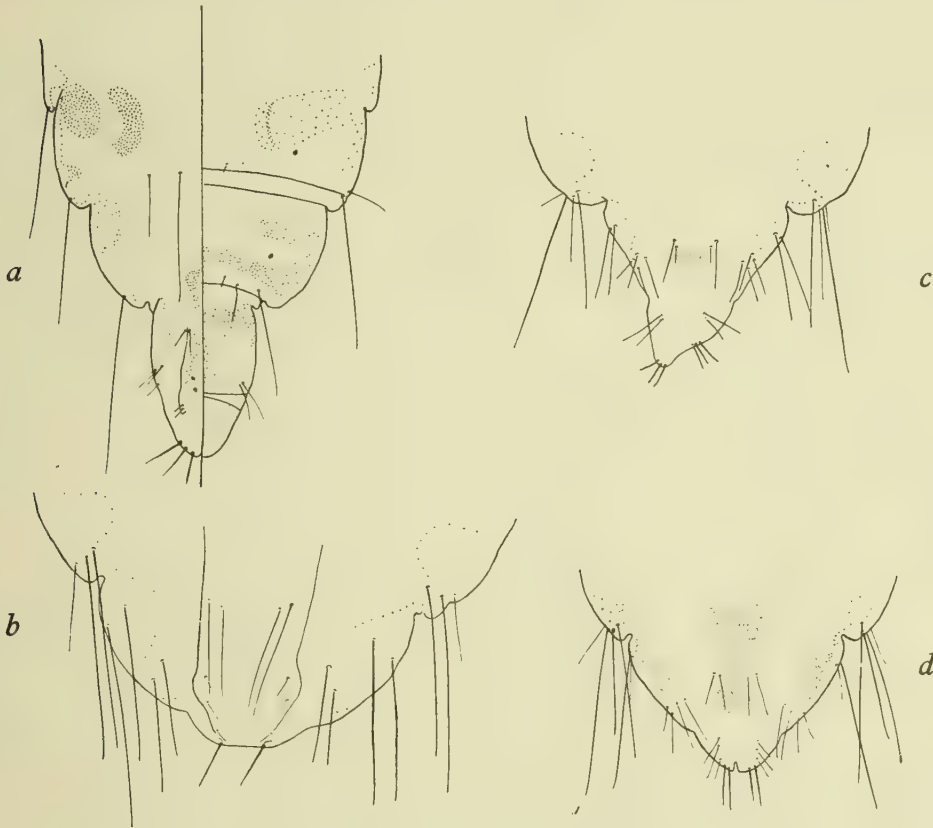
Abdomen similar in general characters to that of *confidens* but somewhat narrower. Vulva and chaetotaxy of genital region as shown in text-fig. 6b. Chaetotaxy as in *confidens*.

MATERIAL EXAMINED: 6 ♂, 15 ♀ from skins of *Diomedea irrorata* Salvin from the Galapagos Islands.

Perineus hyalinus (Neumann) 1911. (Text-figs. 3c, 4b, 5d and 6c)

Lipeurus hyalinus Neumann, 1911, p. 21, pl. ii, f. 1. Type host: *Diomedea exulans* Linné.

Lipeurus nigropunctatus Enderlein, 1917, p. 244, figs. 5-7. Type host: *Diomedea exulans* Linné.



TEXT-FIG. 4.—*Perineus* spp. Terminal segments of ♂ abdomen. (a) *P. diomedae*; (b) *P. hyalinus*; (c) *P. confidens*; (d) *P. obscurus*.

This is a characteristic species distinguished from others of this group by the lack of pigmentation, by the shape of the head, the characters of the terminal segments of the abdomen, in both sexes, and by the male genitalia.

Male.—Head as shown in text-fig. 3c.

Thorax as shown in Neumann's figure with chaetotaxy as in *diomedae*.

Abdomen with general characters as in Neumann's figure. Segments VIII and IX not greatly narrowed as in preceding species and with segment IX small (text-fig. 4b). Chaetotaxy as in *confidens*.

Genitalia distinguished from previous species by the large size, thickened

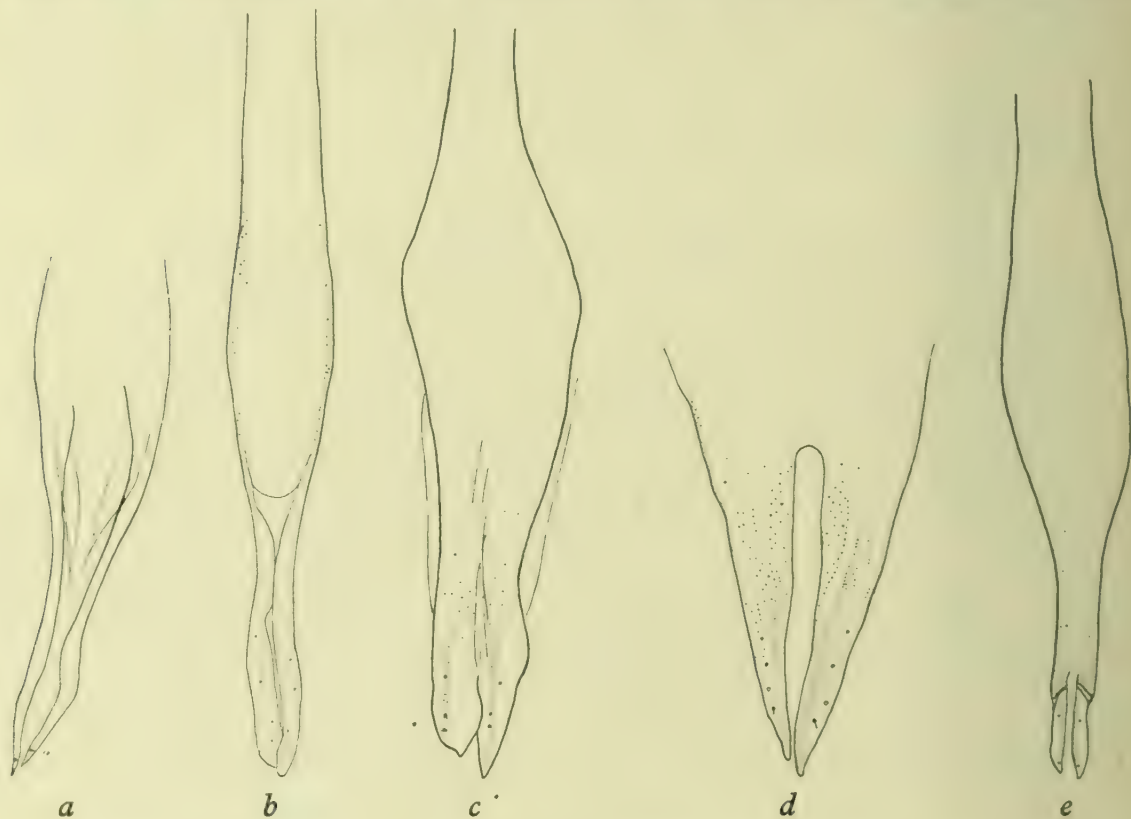
paramera and presence of sac bearing chitinized teeth (text-fig. 5*d*). Total length of genital apparatus is 1.62 mm.

Female.—Head similar to male but of somewhat different proportions and as in all these species the clypeal suture is more obvious than in the male, especially in the median area of head.

Thorax as in male.

Abdomen with general characters as shown in Neumann's figure. Vulva with shape and chaetotaxy distinctive (text-fig. 6*c*). Chaetotaxy as in *confidens*.

MATERIAL EXAMINED: 1 ♂, 1 ♀, Neumann's types from *Diomedea exulans* Linné



TEXT-FIG. 5.—*Perineus* spp. ♂ genitalia. (a) *P. diomedae*; (b) *P. confidens*; (c) *P. miriceps* (d) *P. hyalinus*; (e) *P. obscurus*.

from the S. Indian Ocean (lat. 40° S., long. 47° W.); 1 ♂, 1 ♀ Enderlein's types of *nigropunctatus* from *Diomedea exulans* collected at sea between Kapland and Tristan da Cunha (10.xi.1901); 10 ♂, 19 ♀ from skins and fresh specimens of the same host from N.W. Australia and the Cape.

Perineus giganticola (Kellogg) 1896.

Nirmus giganticola Kellogg, 1896, p. 105, pl. v, f. 6. Type host: *Diomedea albatrus* Pallas.

No material of this species has been examined, but the description and figure indicate that it resembles *hyalinus*. However, the measurements of the male head and figure of the female head show that it is not conspecific with this latter species.

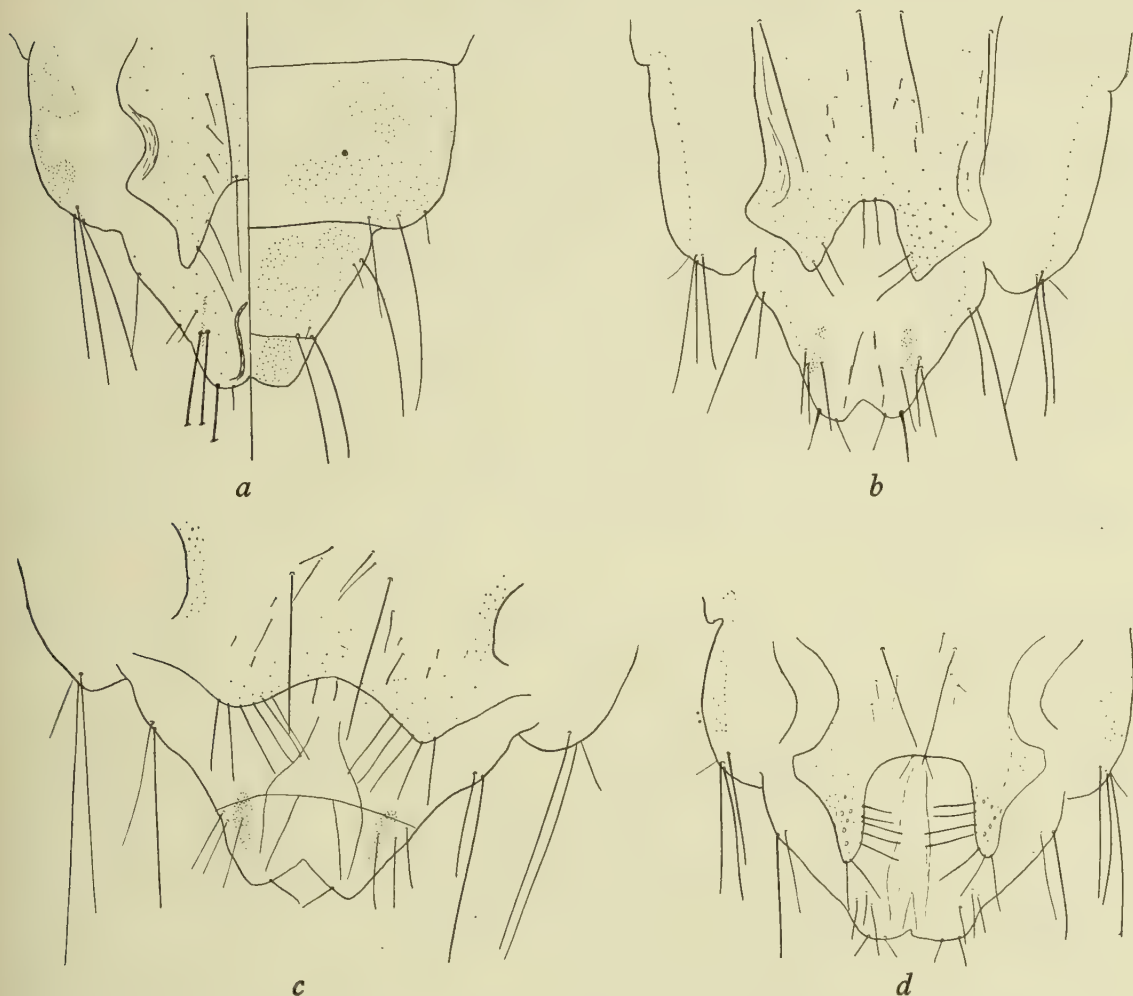
Perineus obscurus (Rudow) 1869. (Text-figs. 3d, 4d, 5c and 6d)

Lipeurus obscurus Rudow, 1869, p. 30. Type host: *Macronectes giganteus* (Gmelin). (*Procellaria gigantea*.)

?*Lipeurus melanocnemis* Giebel, 1874, p. 233. Type host: *Macronectes giganteus* (Gmelin). (*Procellaria gigantea*.)

Lipeurus gaini Neumann, 1913, p. 192, f. 4-5. Type host: *Macronectes giganteus* (Gmelin). (*Ossifraga gigantea*.)

Rudow's original description of *obscurus* has been interpreted by the present author as representing the species described below and a neotype has been designated



TEXT-FIG. 6.—*Perineus* spp. ♀ genital region. (a) *P. diomedae*; (b) *P. miriceps*; (c) *P. hyalinus*; (d) *P. obscurus*.

to fix this name definitely. It has been impossible to obtain information on Giebel's type of *melanocnemis*, but from the description it appears to be conspecific with this species. The types of *gaini* have been examined and found to be conspecific with the species described below.

This species is distinguished by the absence of a definite clypeal suture and by the characters of the terminal segments of the abdomen in both sexes.

Male.—Head as shown in text-fig. 3*d*, and characterized by the shape of the pre-antennal region and absence of definite lateral clypeal suture.

Thorax with shape as shown in Neumann's figure for *gaini* with chaetotaxy as in *diomedae*.

Abdomen with general characters as shown in Neumann's figure; segments VIII and IX not greatly narrowed as in *diomedae*, *confidens*, and *miriceps*. Chaetotaxy of dorsal surface and ventral surface of segments I–VII as in *confidens*; ventral surface of posterior segments as shown in text-fig. 4*d*.

Genitalia with small flattened paramera and lightly armed sac. Total length of the genital apparatus figured in text-fig. 5*e* is 0.95 mm.

Female.—Head similar to that of male, but differing somewhat in shape (see Neumann, f. 5).

Thorax similar to that of male.

Abdomen with general characters as shown in Neumann's figure of *gaini*. Shape and chaetotaxy of vulva characteristic (text-fig. 6*d*).

Dorsal and ventral chaetotaxy of segments I–VI as in *confidens*, but on the ventral surface segment I has apparently only 2 central hairs.

MATERIAL EXAMINED: 22 ♂, 33 ♀ from skins and fresh specimens of *Macronectes giganteus* (Gmelin) from Cape Seas, Peru, Chile, and S. Georgia.

Types of *gaini* Neumann: 1 ♂, 1 ♀, slide No. 410, from *Ossifraga gigantea* (*Macronectes giganteus*) from Petermann Island.

Neotype designated by present author: ♂ in the Meinertzhagen Collection, slide No. 12688, from *Macronectes giganteus* from Chile. *Neoparatypes*: 21 ♂, 33 ♀ in the Hopkins and Meinertzhagen Collections from the same host from various localities.

MEASUREMENTS

MALES

		<i>diomedae</i>	<i>confidens</i>	<i>miriceps</i>	<i>hyalinus</i>	<i>obscurus</i>
		mm.	mm.	mm.	mm.	mm.
<i>Length</i> :						
Head (a)*	..	0.66–0.71	0.75–0.78	0.75–0.80	0.86–0.88	0.77–0.81
(b)	..	0.23–0.25	0.29–0.31	0.29–0.31	0.29–0.31	0.32–0.34
Prothorax	..	0.16–0.23	0.23–0.25	0.23–0.25	0.26–0.31	0.21–0.23
Pterothorax	..	0.45–0.47	0.57–0.61	0.51–0.54	0.75–0.77	0.46–0.52
Abdomen	..	1.49–1.68	1.77–1.92	2.10–2.22	2.60–2.64	1.60–1.65
Total	..	2.80–2.85	3.22–3.50	3.60–3.65	4.40–4.45	2.98–3.12
<i>Breadth</i> :						
Head (a)*	..	0.49–0.55	0.57–0.60	0.49–0.50	0.85	0.60–0.63
(b)	..	0.26–0.29	0.31–0.32	0.29–0.32	0.40–0.43	0.37–0.41
Prothorax	..	0.38–0.40	0.50–0.52	0.46–0.48	0.58	0.41–0.46
Pterothorax	..	0.47–0.49	0.66–0.69	0.53–0.55	0.95	0.54–0.58
Abdomen	..	0.52–0.55	0.75–0.80	0.78–0.80	1.86	0.68–0.69
C.I. (a)	0.74–0.79	0.74–0.78	0.62–0.66	0.96–0.99	0.76–0.80
(b)	1.13–1.18	1.00–1.11	0.95–1.04	1.34–1.47	1.09–1.28

		FEMALES				
		<i>diomedea</i>	<i>confidens</i>	<i>miriceps</i>	<i>hyalinus</i>	<i>obscurus</i>
		mm.	mm.	mm.	mm.	mm.
<i>Length:</i>						
Head (a)	..	0.74-0.75	0.80-0.83	0.75-0.77	0.86-0.88	0.74-0.85
(b)	..	0.24-0.25	0.34-0.35	0.32-0.34	0.40-0.41	0.35-0.37
Prothorax	..	0.17-0.22	0.23-0.25	0.23	0.26	0.20-0.22
Pterothorax	..	0.46-0.49	0.60-0.62	0.51	0.77	0.40-0.57
Abdomen	..	2.18-2.30	2.46-2.48	2.36	2.40	1.95-2.18
Total	..	3.48-3.60	3.80-4.00	3.70	4.20	3.24-3.70
<i>Breadth:</i>						
Head (a)	..	0.57-0.61	0.67-0.69	0.54-0.55	0.83-0.89	0.65-0.74
(b)	..	0.32-0.34	0.34-0.37	0.31-0.32	0.40-0.41	0.38-0.41
Prothorax	..	0.39-0.41	0.46-0.49	0.41-0.43	0.55-0.63	0.46-0.55
Pterothorax	..	0.47-0.55	0.68-0.71	0.50-0.51	0.80-0.87	0.63-0.71
Abdomen	..	0.80-0.83	0.94-1.08	0.71-0.73	1.03-1.17	0.90-0.92
C.I. (a)	..	0.77-0.82	0.83-0.86	0.71-0.73	0.93-1.03	0.87-0.88
(b)	..	1.05-1.11	1.00-1.09	0.91-1.00	1.08-1.16	1.11-1.22

* Length (a) = total length of head. Length (b) = length of lateral margin of head from postero-lateral termination of antennal band to anterior termination of clypeal band.

Breadth (a) = breadth at temples. Breadth (b) = breadth of head at hair arising immediately anterior to origin of clypeal suture.

Genus *Naubates* Bedford

The species of Esthiopterinae from the Procellariformes, as in other groups of species from single orders of birds, appear at first sight, to be divisible into a number of well-defined though related genera. However, when a large amount of material is examined a number of species arise, showing intermediate characters which necessitates either the suppression of some of the genera or the endless formation of new genera, often monotypic, to include these intermediates. This latter course does not clarify the classification and merely obscures the natural relationships between the species.

Having examined a considerable amount of material, there appears to the author to be little doubt that *Synautes* is inseparable from *Halipeurus*. Typical *Synautes* species, according to Thompson (1936, p. 43 and 1939, pp. 118 and 119) are distinguished from typical *Halipeurus* by their slender form, scaly cuticle, short internal bands and more strongly developed ventral bands. However, a new species from *Nesofregetta albigularis*, Pl. I, f. 1 (females only examined) shows the characters of typical *Synautes* in the slender form, scaly cuticle, and well-developed ventral bands, but resembles *Halipeurus* in that the internal bands reach to the level of the mandibles. A species from *Bulweria bulwerii*, Pl. I, f. 3, has the characters of typical *Halipeurus* but is more slender in form than *S. pelagicus* (Denny). In some of the species from *Pterodroma*, in which the characters are mainly those of typical *Halipeurus*, the ventral bands appear more prominent than usual, and in some of the species from *Puffinus* the cuticle may be partly scaly. A new species from *Oceandroma macrodactyla*, Pl. I, f. 2, a stout form resembling the largest of the typical *Halipeurus* in size, has the scaly

cuticle and the ventral and internal bands as in typical *Synautes* but has no lateral indication of the clypeal suture, thus resembling the new species *garrodiae* described below. When all these species are considered there does not seem to be any characters on which *Synautes* and *Halipeurus* can be satisfactorily separated.

Typical *Naubates* species appear distinct from those of *Halipeurus* mainly due to the greater development of the ventral bands, the larger size of the clypeal suture, and the form of the clypeal signature. However, species from *Haloboena* and *Pachyptila* do not have the ventral bands greatly developed, and there is a certain amount of variation in the size of the clypeal suture throughout typical *Halipeurus* species and in the form of the signature throughout *Naubates* species. The characters of the two new species described below, in which the signature and male abdomen resembles to a certain extent those of *Naubates* and the pre-antennal bands and female abdomen resemble those of typical *Synautes*, taken in conjunction with the facts discussed above, indicate that it is more satisfactory to keep all *Halipeurus* and *Synautes* species in *Naubates* instead of describing new genera to include the atypical species. It is apparent from these species that certain characters such as the presence or absence of the lateral indication of the clypeal suture are not of generic importance, and that these species have been divided into genera not so much on the absence and presence of characters but on the relative development of characters which are present in all the species.

In this discussion *Philoceanus* has not been mentioned, although it is closely related to *Naubates*, but the presence of the labral expansion and the characters of the dorsal antennal bands and lateral articulation of the mandible are distinctive. However, in the two latter characters and in the characters of the clypeal signature and absence of clypeal suture the species *annuliventris* appears to form a link between *garrodiae* and *Philoceanus*.

In considering *Naubates* it might be mentioned that the subgenus *Micronaubates* Pessoa and Guimarães with *garbei* Pessoa and Guimarães as genotype which was included in *Naubates* by Thompson (1938¹, p. 486) should be included as a synonym of *Pectinopygus*.

Naubates garrodiae, sp. n. (Text-figs. 7, 8, 9a and d, and 11a).

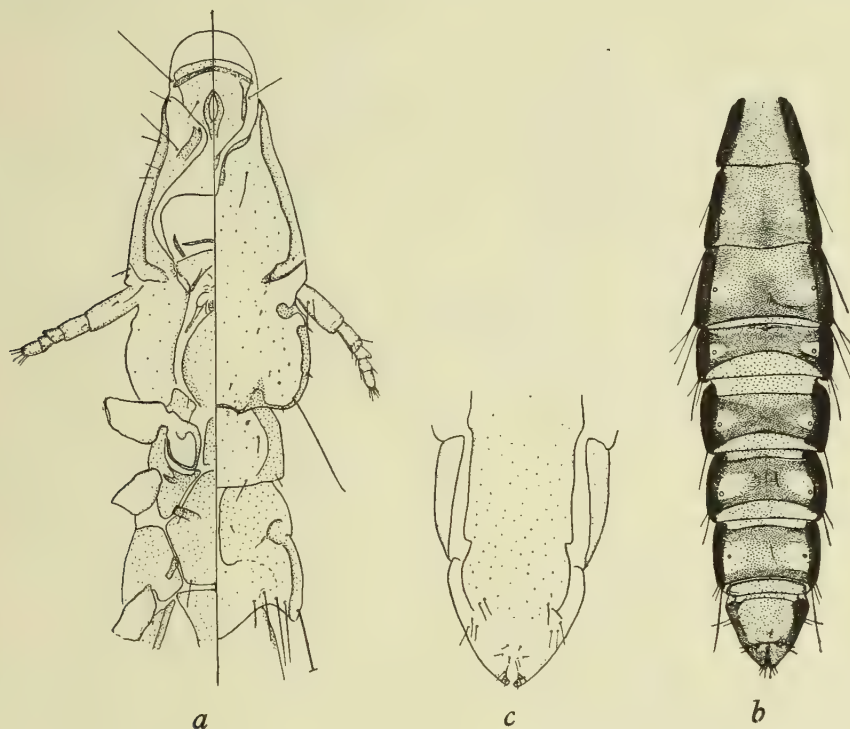
21 ♂, 22 ♀, 11 immature from *Garrodia nereis* (Gould), Kidney Island, E. Falkland.

Giebel (1874, p. 236) originally described *Lipeurus clypeatus* from *Halobaena caerulea* (Gmelin) (*Pachyptila coerulescens*); Taschenberg (1882, p. 154, Pl. V, f. 2) re-described and figured this species, presumably from Giebel's original specimens, showing a species with definite clypeal suture and internal bands; Giebel (1876, p. 389) refers to *L. clypeatus* collected from *Garrodia nereis* (Gould) (*Procellaria nereis*), and in 1878, p. 255, gives a further description and figure of these specimens. It is apparent from the figure (1878, Pl. XIV, f. 20) and from a single female in the British Museum from *Procellaria nereis* collected by the Rev. A. E. Eaton at Kerguelen Island in 1876 and presumably part of the material examined by Giebel, that these specimens are conspecific with *garrodiae* and not with *L. clypeatus*.

This species is distinguished from *robertsi*, sp. n., and *annuliventris* Uchida, by

the proportions of the head and male genitalia and from *anuliventris* also by the character of the antennal bands.

Male.—Head with broad hyaline margin; elongated somewhat pointed pre-antennal region; clypeal signature well-defined with distinct central gutta and lateral pear-shaped incrassations; antennal band continuous with clypeal band, there being no suture; ventral plate with short thickened bands anteriorly; internal bands short; large thickened occipital signature present. Antennae with segment I not greatly enlarged and with distal pre-axial angle of segment III prolonged slightly (text-fig. 7a).



TEXT-FIG. 7.—*Naubates garrodiae* ♂. (a) Head and thorax; (b) Abdomen; (c) Terminal segments of abdomen, ventral.

Prothorax small; meso-metathorax elongated with posterior margin pointed medianly; mesonotum with median division; prosternal plate narrow and elongate; meso-metasternal plate roughly hexagonal in shape and joined to the bell-shaped first abdominal sternal plate by a narrow chitinous bar.

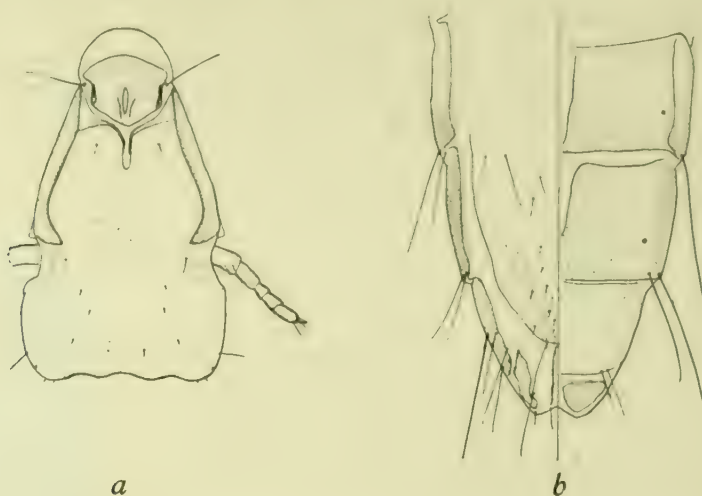
Abdomen elongated with segment V–VI modified (text-fig. 7b); last segment pointed posteriorly and medianly emarginate. Sternal thickening in the form of median plates. Tergal plates I–IV with a minute hair each side; sternal plates I–VII with two hairs each side; segments I–VII with one lateral hair each side. Ventral chaetotaxy of posterior segments as in text-fig. 7c.

Genitalia with paramera flattened and unthickened (text-fig. 11a). Total length of genital apparatus 0.99 mm.

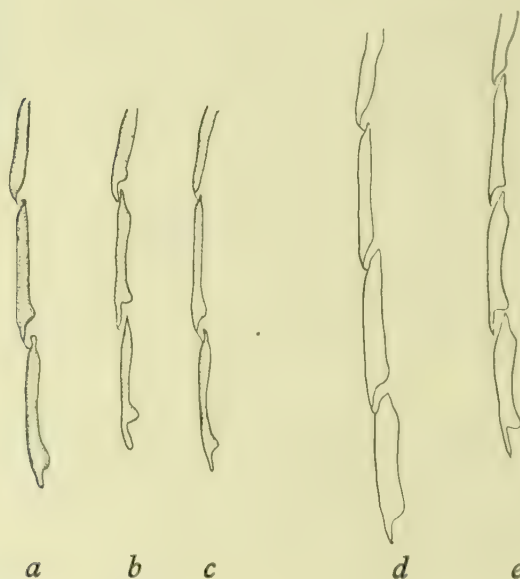
Female.—Head similar to that of male but proportions somewhat different (text-fig. 8a).

Thorax as in male.

Abdomen elongated, somewhat broader than that of male, and showing differences in the characters of the tergal and paratergal plates. Paratergal plates with straight internal margins without inwardly directed processes as in segments IV–VII of male abdomen (text-figs. 9*a* and *d*). Tergal plates I–VII either partially or completely



TEXT-FIG. 8.—*Naubates garrodiae* ♀. (a) Head; (b) genital region.



TEXT-FIG. 9.—Paratergal plates of *Naubates* spp. (a) ♂ *N. garrodiae*; (b) ♂ *N. annuliventris*; (c) ♂ *N. robertsi*; (d) ♀ *N. garrodiae*; (e) ♀ *N. annuliventris*.

divided medianly. Posterior margin of terminal segment emarginate; vulva simple and bearing a few scattered hairs (text-fig. 8*b*). Chaetotaxy of segments I–VI as in male.

Holotype: ♂ in the British Museum Collection, slide No. 71, from *Garrodia nereis* (Gould) from Kidney Island, E. Falklands. *Paratypes*: 20 ♂, 22 ♀ from the same host.

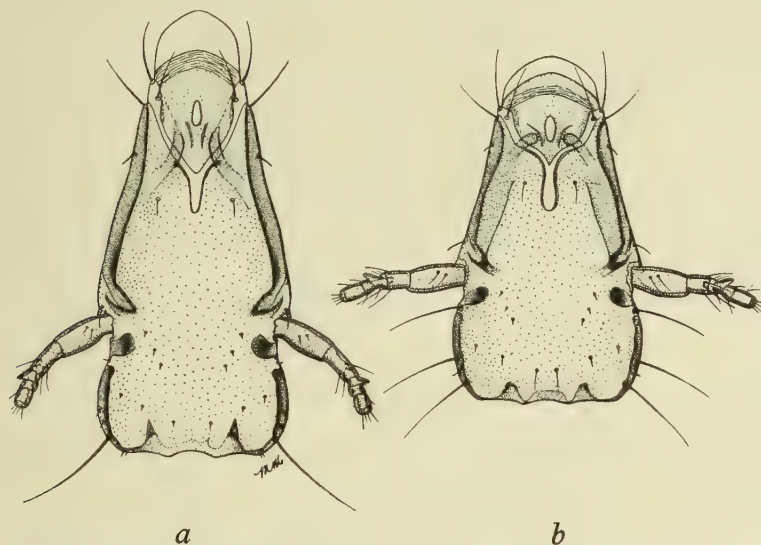
Naubates robertsi, sp. n. (Text-figs. 9c, 10a and 11b)

6 ♂, 2 ♀ collected from the underside of wings of 4 specimens of *Oceanites oceanicus exasperatus* Mathews, Argentine Islands, W. Graham Land.

This species is distinguished from *garrodiae* by the shape of the head, the pre-antennal region being proportionally longer, and by the male genitalia.

Male.—Head as shown in text-fig. 10a,¹ with general characters as in *garrodiae*. Thorax as in *garrodiae*.

Abdomen similar to that of *garrodiae* but tends to be somewhat shorter and the terminal segment less pointed posteriorly. Chaetotaxy as in *garrodiae*.



TEXT.-FIG. 10.—♂ heads. (a) *N. robertsi*; (b) *N. annuliventris*.

Genitalia similar to those of *garrodiae* but are smaller and less heavily pigmented and the sac is apparently absent (text-fig. 11b). Total length of genital apparatus is 0.71 mm.

Female.—Head similar to male, but differs somewhat in shape (compare measurements).

Thorax as in male.

Abdomen similar to that of *garrodiae* but tends to be somewhat narrower. Vulva as in *garrodiae* but is somewhat more pointed posteriorly and the two specimens of *robertsi* examined have fewer hairs. Chaetotaxy of abdomen as in *garrodiae*.

Holotype: ♂ in the British Museum Collection, slide No. 85, from *Oceanites oceanicus exasperatus* Mathews, from Argentine Island, W. Graham Land. *Paratypes*: 5 ♂, 2 ♀.

The species is named in honour of Mr. Brian Roberts, who made this collection of Mallophaga from the Antarctic.

Two other species have been recorded from *Oceanites oceanicus*, namely *languidus* Kellogg and Kuwana, and *exiguus* Kellogg and Kuwana. The former species is a typical *Synautes*, the latter probably an immature form of the same species.

¹ Figure shows dorsal view but also indicates position of ventral bands.

Naubates annuliventris (Uchida) 1917 (Text-figs. 9*b* and *e*, 10*b* and 11*c*)

Lipeurus annuliventris Uchida, 1917, p. 206, f. 2. Type host: *Oceanodroma furcata* (Gmelin).

This species is distinguished from both *garrodiae* and *robertsi* by the shape of the head and by the presence of a wide dorsal antennal band.

Male.—Head as shown in text-fig. 10*b*, with general characters as in the two preceding species except for the presence of a broad dorsal antennal band.

Thorax as in *garrodiae*.



TEXT-FIG. 11.—♂ genitalia. (a) *N. garrodiae*; (b) *N. robertsi*; (c) *N. annuliventris*.

Abdomen similar to that of *garrodiae* but with differences in the outline of paratergal plates I–III (text-fig. 9*b*). Terminal segment not pointed posteriorly as in *garrodiae*. Chaetotaxy as in *garrodiae*.

Genitalia similar to those of the two preceding species, but the paramera are more heavily chitinated and the sac is more heavily armed (text-fig. 11*c*). Total length of genital apparatus is 0.85 mm.

Female.—Head with general characters as in male, but differs somewhat in shape (see measurements).

Thorax as in male.

Abdomen similar to that of *garrodiae*, but with differences in the outline of paratergal plates (text-fig. 9*e*). Vulva as in *garrodiae* but more pointed posteriorly. Chaetotaxy as in *garrodiae*.

MATERIAL EXAMINED: 2 ♂, 3 ♀ from skin of *Oceanodroma furcata* from Alaska.

MEASUREMENTS

MALES

			<i>garrodiae</i>	<i>robertsi</i>	<i>annuliventris</i>
			mm.	mm.	mm.
<i>Length:</i>					
Head (a)*	0.57-0.63	0.63-0.67	0.54
(b)	0.40-0.41	0.43-0.44	0.31
Prothorax	0.10-0.12	0.14-0.15	0.14
Pterothorax	0.22-0.25	0.22-0.24	0.20
Abdomen	1.48-1.51	1.39-1.41	1.38
Total	2.34-2.36	2.48-2.50	2.24
<i>Breadth:</i>					
Head (a)*	0.29-0.31	0.28-0.29	0.31
(b)	0.29-0.31	0.28-0.29	0.28
Prothorax	0.22-0.23	0.21-0.23	0.22
Pterothorax	0.27-0.30	0.27-0.29	0.29
Abdomen	0.35-0.40	0.36-0.37	0.37
C.I. (a)	0.48-0.51	0.42-0.44	0.57
(b)	0.70-0.75	0.65	0.90

FEMALES

<i>Length:</i>					
Head (a)	0.57-0.61	0.61-0.63	0.54-0.55
(b)	0.37-0.38	0.38-0.41	0.31-0.34
Prothorax	0.12-0.15	0.15	0.12
Pterothorax	0.28-0.30	0.26	0.26
Abdomen	1.63-1.71	1.67	1.50
Total	2.52-2.78	2.60	2.30
<i>Breadth:</i>					
Head (a)	0.34-0.35	0.33-0.34	0.31-0.32
(b)	0.31-0.32	0.30-0.31	0.28
Prothorax	0.23-0.25	0.23	0.23
Pterothorax	0.30-0.32	0.29	0.28
Abdomen	0.44-0.47	0.45	0.43
C.I. (a)	0.56-0.61	0.52-0.55	0.57
(b)	0.81-0.86	0.75-0.81	0.85-0.91

* Length (a) = total length of head. Length (b) = length of pre-antennal region.

Breadth (a) = greatest breadth of post-antennal region. Breadth (b) = greatest breadth of pre-antennal region.

Naubates sp.?

Two immature ♀ from under wing of 2 specimens of *Puffinus griseus* (Gmelin), Kidney Island, E. Falkland.

These specimens belong to a species of the typical *Halipeurus* group, but are too immature to identify specifically.

LIST OF SPECIES OF ANOPLURA COLLECTED BY THE BRITISH GRAHAM
LAND EXPEDITION

SPECIES	HOST
<i>Antarctophthirus lobodontis</i> Enderlein.	<i>Lobodon carcinophagus</i> (Jacquinot and Pucheran).
<i>Antarctophthirus</i> sp. ?	<i>Leptonychotes wedelli</i> (Lesson).
<i>Menopon becki</i> Kellogg.	<i>Phaethon a. aethereus</i> Linné.
<i>Tetrophthalmus</i> sp. ?	<i>Phalacrocorax a. atriceps</i> King.
	<i>Phalacrocorax a. albiventer</i> (Lesson).
? <i>Austrogoniodes hamiltoni</i> Harrison.	<i>Eudyptes c. cristatus</i> (Miller).
<i>Philopterus bicolor</i> (Rudow).	<i>Priocella antarctica</i> (Stephens).
<i>Philopterus</i> spp. ?	<i>Daption capensis</i> (Linné).
? <i>Philopterus platycephalus</i> (Kellogg & Kuwana).	<i>Garrodia nereis</i> (Gould).
<i>Docophoroides brevis</i> (Dufour).	<i>Diomedea exulans</i> Linné.
<i>Docophoroides harrisoni</i> Waterston.	<i>Diomedea m. melanophris</i> Temminck.
<i>Pseudonirmus gurlti</i> (Taschenberg).	<i>Daption capensis</i> (Linné).
<i>Episbates pederiformis</i> (Dufour).	<i>Diomedea exulans</i> Linné.
? <i>Harrisionella ferox</i> (Giebel).	<i>Diomedea exulans</i> Linné.
<i>Perineus diomedeeae</i> (Fabricius).	<i>Diomedea m. melanophris</i> Temminck.
<i>Perineus nigrolimbatus</i> (Giebel).	<i>Priocella antarctica</i> (Stephens).
<i>Naubates garrodiae</i> , sp. n.	<i>Garrodia nereis</i> (Gould).
<i>Naubates robertsi</i> , sp. n.	<i>Oceanites oceanicus exasperatus</i> Mathews.
<i>Naubates</i> sp. ?	<i>Puffinus griseus</i> (Gmelin).

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* The greater part of this paper was taken from Harrison's manuscript, see Harrison, 1937.

PLATE I.

FIG. 1.—*Naubates* sp. from *Nesofregatta albigularis*.

FIG. 2.—*Naubates* sp. from *Oceandroma macrodactyla*.

FIG. 3.—*Naubates* sp. from *Bulweria bulweri*.



Fig. 1



Fig. 2



Fig. 3

BRITISH MUSEUM (NATURAL HISTORY)

BRITISH GRAHAM LAND EXPEDITION

1934-37

SCIENTIFIC REPORTS

Volume I, No. 6, pp. 319-322

LOWER CRUSTACEA

By

J. P. HARDING, F.R.S.

British Museum (Natural History)

WITH NINE TEXT FIGURES

LONDON

PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

LOWER CRUSTACEA

By J. P. HARDING, Ph.D.

British Museum (Natural History)

(With nine text-figures)

DR. COLIN BERTRAM has kindly allowed me to examine the Entomostraca collected by him in Graham Land and South Georgia. In addition to the material from the British Graham Land Expedition 1934-37 a few tubes from the *Discovery* Investigations in the same region have been included. It is convenient to deal with them all together here.

The following species were found:

Anostraca,

Branchinecta gaini Daday.

Cladocera,

Macrothrix hirsuticornis (Norman & Brady).

Copepoda,

Pseudoboeckella poppei Mrázek.

Pseudoboeckella silvestri Daday.

Parabroteas sarsi (Daday).

Harpacticus furcatus Lang.

Although the collection is a small one and consists mostly of well-known species, the material is of much interest as it shows a considerable southward extension of the range of several of the species. Various forms previously recorded from South Georgia, a relatively sub-polar region, are now known to occur far to the south on the west coast of Graham Land in a climate that is very much more severe. Of particular interest in this connection is the genus *Pseudoboeckella*.

The group of genera to which *Pseudoboeckella* belongs occurs in S. America and Australia, and Marsh (1924) has suggested that the centre of distribution of these genera was on the Antarctic Continent. If this is so species such as *Pseudoboeckella poppei* and *P. silvestri*, which are now found to occur in Graham Land and which were previously known from Patagonia and South Georgia, may have extended their range from Graham Land to Patagonia rather than in the reverse direction.

Branchinecta gaini Daday

This Antarctic species was found at the following fresh-water stations near the west coast of Graham Land: Galindez Island (Stn. 602), Bay Island, Léonie Island

(Stn. 1448), Horseshoe Harbour (Stn. 1561); and also farther north in the South Shetlands on the lower slopes of the Ullman range 200 feet above sea-level (Stn. 1481 of the *Discovery* Investigations).

DISTRIBUTION: It has previously been found in South Georgia and Graham Land.

Macrothrix hirsuticornis (Norman & Brady)

Four specimens of this species were found in fresh water at Horseshoe Harbour (Stn. 1561) with *Branchinecta gaini* and *Pseudoboeckella poppei*.

Ekman (1905) found specimens of *Macrothrix hirsuticornis* in material from South Georgia.

DISTRIBUTION: Arctic regions, Europe, Syria, Algeria, Central Asia, N. America, Argentina, Falkland Islands, South Georgia, and now Graham Land.

Pseudoboeckella poppei Mrázek

Four adult males and many immature specimens of both sexes were found in fresh water at Horseshoe Harbour (Stn. 1561). Three males were also found in South Georgia (Stn. 1589).

DISTRIBUTION: The species has previously been recorded from South Georgia and Patagonia.

Pseudoboeckella silvestri Daday

A few specimens of both sexes in rather poor condition were found in the *Discovery* Investigations (Stn. 1481) on the slopes of the Ullman range in the South Shetlands.

The males differ from Daday's description of the type in having the left fifth endopod divided into three segments instead of two.

DISTRIBUTION: If *Pseudoboeckella entzii* Ekman non Daday is included as is suggested by Marsh (1924) this species has previously been found in Patagonia, Falkland Islands, South Georgia, and Louis-Philipe Land.

Parabroteas sarsi (Daday)

syn. *Limnocalanus sarsi* Daday 1901.

Parabroteas michaelsoni Mrázek 1901.

Gigantella sarsi Ekman 1905.

Parabroteas sarsi Sars 1909.

Seven females were found in Station 1589 in South Georgia.

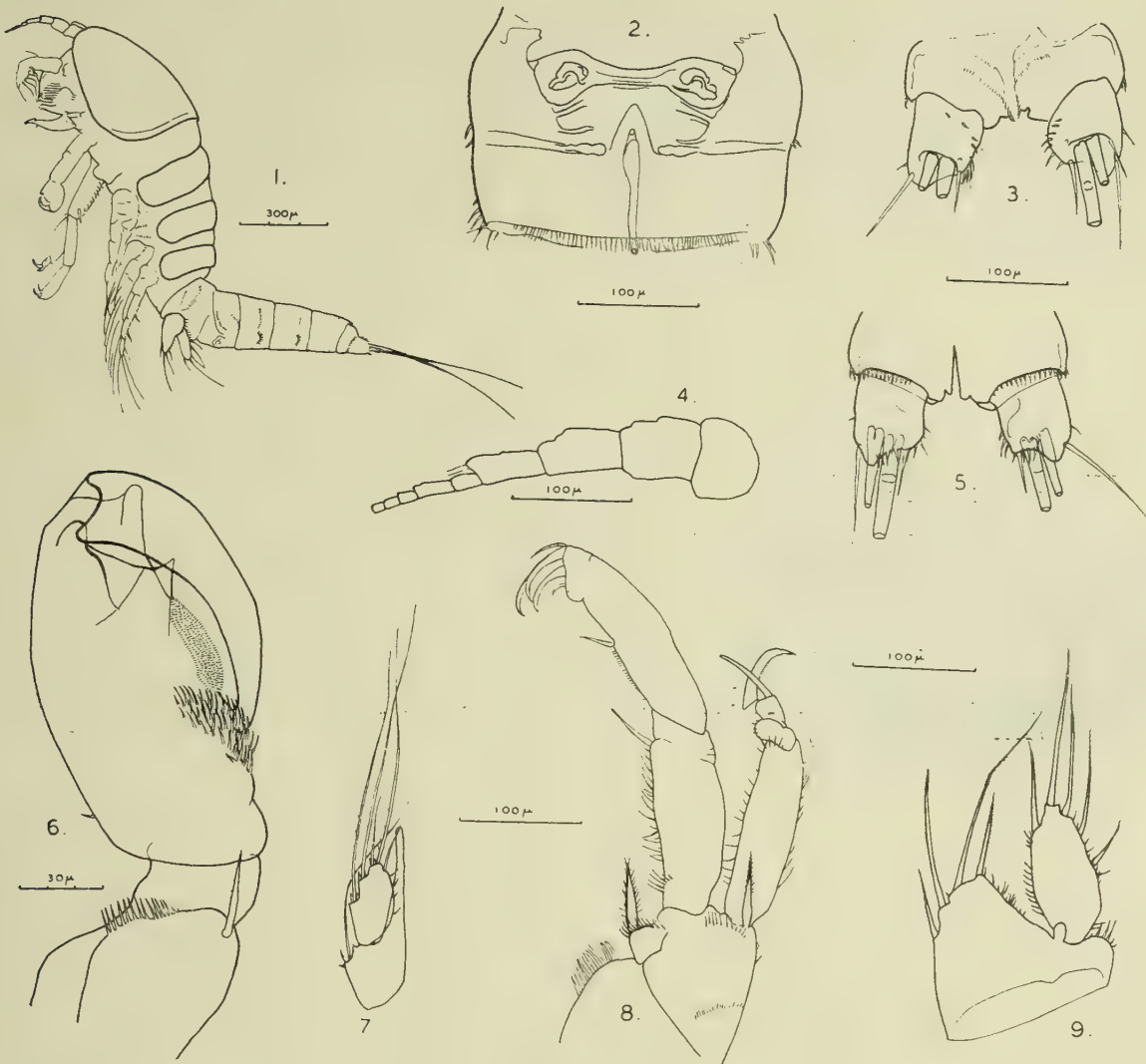
DISTRIBUTION: Previously recorded from Patagonia, Falkland Islands, South Georgia.

Harpacticus furcatus Lang

syn. *Harpacticus chelifera* Giesbrecht non Müller.

Many specimens of both sexes were found "in swarms in depressions at the bottom of a fresh-water pool just above high water of spring tides, no doubt salt at times" in False Island, Station 1431. (False Island is north of Antwerp Island and almost in de Gerlache Strait.)

Many of the females carried egg-sacs. There were also many males, some of which were copulating with smaller females than those with egg-sacs and which appeared to be immature.



FIGS. 1-9. *Harpacticus furcatus* Lang.

- | | |
|-------------------------------|--|
| 1. Adult female. | 6. Maxillipede. |
| 2. Genital somite, female. | 7. Leg 2, male, endopods 2 and 3. |
| 3. Furcal rami, dorsal view. | 8. Leg 1, female. Claw of endopod displaced. |
| 4. Antennule, female. | 9. Leg 5, female. |
| 5. Furcal rami, ventral view. | |

The specimens agreed closely with the description and figures of the Antarctic form called *H. chelifera* by Giesbrecht (1902). Lang (1936) described *H. furcatus* also from the Antarctic which he considers is the same as Giesbrecht's *H. chelifera*. Lang's figures of *H. furcatus* are however somewhat diagrammatic, and until I saw the types I thought they could not be of the same species as the specimens I had before me. However, thanks to Prof. Sixten Bock of the Stockholm Museum, I have been able

to examine the types and it is clear that the Graham Land Expedition specimens are Lang's *Harpacticus furcatus*, and that Lang is correct in saying that this species is the same as Giesbrecht's *H. chelifer*.

DISTRIBUTION: de Gerlache Strait, Bransfield Strait, Cumberland Bay, South Georgia. All these localities are in the Antarctic and most specimens have been found in salt water. Lang found some under stones near low water mark. The genus *Harpacticus* is almost exclusively marine, though many species are littoral in habitat and some are found in brackish water. Dr. Bertram assures me that the pool from which the specimens were taken was above high water of Spring tides and was completely fresh to taste at the time of collection, though it would often be made salt by spray.

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BRITISH MUSEUM (NATURAL HISTORY)

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SPHAEROCERIDAE (DIPTERA)

By

O. W. RICHARDS, M.A., D.Sc.

WITH ONE TEXT FIGURE

LONDON

PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

MADE AND PRINTED IN GREAT BRITAIN BY
JARROLD AND SONS, LTD., NORWICH AND LONDON

SPHAEROCERIDAE (DIPTERA)

Collected by the British Graham Land Expedition, 1934-37

By O. W. RICHARDS, M.A., D.Sc.

(With one text-figure)

THE members of the British Graham Land Expedition in the *Penola* called at a number of islands in the Antarctic and insects were collected on some of them. Dr. John Smart (British Museum (Natural History)) has kindly handed over the Sphaeroceridae to me for study. All the specimens recorded below are preserved in the British Museum.

Leptocera Olivier, 1813

L. (Leptocera) caenosa (Rondani, 1880)

SOUTH SHETLANDS: Deception Island, 10.i.1936, 2 ♂ 2 ♀.

These specimens are in bad condition and are preserved in alcohol, but the identification is certain. The species has already been recorded by Duda (1925) from Chile, Peru, and Bolivia. As it is sometimes found in houses, it is probably liable to be spread by ships. The above examples were found in a dirty mug in a house. The females show none of the characters which Duda (*l.c.*) gives for the doubtfully distinct S. American form *L. (L.) aequilimbata* (Duda, 1925).

L. (Limosina) mediospinosa (Duda, 1925)

6 ♂ 2 ♀ with the same data as the preceding.

This species has a very wide distribution, being recorded from Africa, Australia, and S. America. It was not previously known from the Antarctic.

L. (Limosina) pectinifera (Villeneuve, 1917)

FALKLAND ISLANDS: Rabbit Grove, nests of *Pygoscelis papua* (Forster), 18.iv.1936, 8 ♂ 9 ♀; Gentoo Penguin rookery, 28.vii.1936, 14 ♂ 10 ♀.

This species was previously known only as a rare European one, the total number of specimens recorded previously being not much greater than that noted here. As it is sometimes found in houses, it is possible that it was transported to the Antarctic in a ship.

Archiborborus Duda, 1921

A. (Archiborborus) hirtipes (Macquart, 1843)

FALKLAND ISLANDS: Rabbit Cove, Gentoo Penguin rookery (*Pygoscelis papua* (Forster)), 28.vii.1936, 1 ♀.

This species has already been recorded from the Falklands.

A. (Procopromyza) albicans Richards, 1931

FALKLAND ISLANDS: Rabbit Cove, Gentoo Penguin rookery, 28.vii.1936, 1 ♂ 8 ♀ (all the species from this locality were from one nest); SOUTH SHETLANDS: Deception Islands, under timber on whaling ship, 3 ♂ 1 ♀ and 6 unsexed (mouldy).

The species was previously recorded from Chile and Cape Horn.

Penola gen. n.

Wings represented by a bristly, sclerotized rod, as long as width of scutellum and about seven times as long as broad. Halteres absent. Eyes large, considerably longer than broad. Ocelli, especially the anterior one, very small. Five small interfrontals, one preocellar, three superior orbitals, one external vertical, one divergent postocellar (cf. p. 326) on each side. Mesonotum a little narrower than head with eyes, one moderate humeral, one very strong notopleural, two small postalar on each side. Scutellum nearly three times as broad as long, with four widely spaced, small bristles; one strong sternopleural. Mid tibiae with one antero-ventral, one preapical dorsal and an apical ring of bristles (better developed ventrally). Hind tibiae with a long preapical dorsal bristle and two small, spine-like, apical ventral bristles. Abdomen strongly flattened, pyriform, posteriorly truncate, about half as long again as broad, and about two-and-a-half times as broad as thorax, margin sharp, deflexed; sternites very broad, moderately sunk into the tergites; first tergal plate (= I + II) not conspicuously constricted anteriorly to form a neck, only that part of it which belongs to tergite II with a margin.

Genotype *Penola eudyptidis* sp. n.

Penola eudyptidis sp. n.

Female (*ex* alcohol). Pale yellow brown, vertex and mesonotum somewhat more orange-tinted, cerebral region of head and central third of mesonotum on its anterior two-thirds, darker reddish-brown; abdomen shining black, with a faint violet reflection.

Length 2.75 mm.

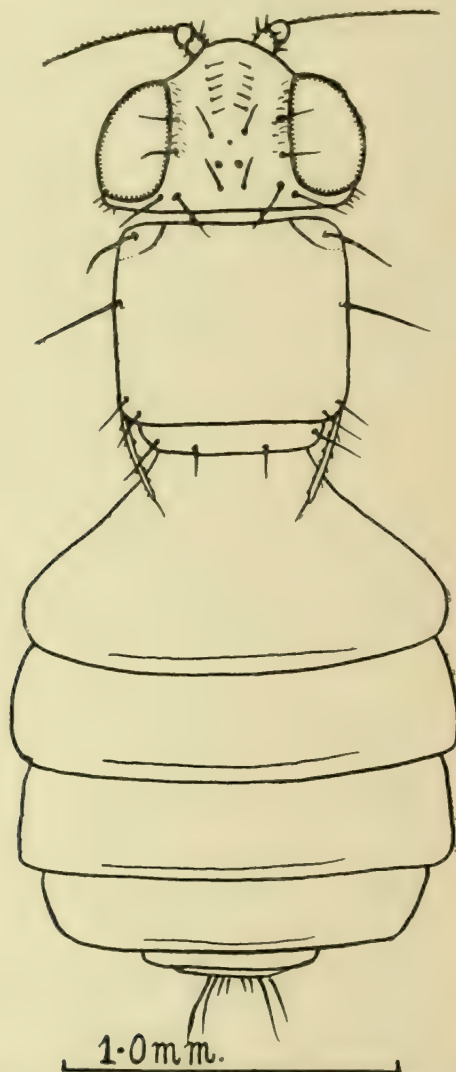
Head with mouth-cavity very large, mouthparts normally large, palpi a little clavate with short, black bristles; vibrissa as long as width of vertex, a row of fine hairs along the oral margin, those nearest to the vibrissa hardly one-quarter its length, jowls otherwise only with fine tomentum; jowls dull, not striate, at vibrissal angle not quite as broad as height of third antennal segment, about three times as wide posteriorly, oral margin with no raised border, angle between it and occiput rounded; eyes quite large, longitudinal diameter nearly twice the vertical one, which is not quite as long as greatest height of jowls, eye in outline an almost regular oval; ocelli small, the anterior one very reduced, the posterior pair situated almost half-way between occiput and frontal suture; face dull, vertical, moderately excavated, mouth-edge hardly prominent, facial "knob" not developed; antennae with third segment suboval, arista two-and-a-half times as long as antennae, with short pubescence; vertex rather dull with orbits, central triangle and a small triangle behind the ocelli more shining; central triangle extending to the suture anteriorly, three

times as long as broad; head on each side with the following bristles, five weak interfrontals, two moderately strong, anterior, outwardly directed superior orbitals, a moderate, inwardly directed, posterior superior orbital placed rather far back, a moderate outwardly directed external vertical, a moderate postocellar (the pair is just divergent), a moderate divergent preocellar; postoculars are just discernible and there are some minute bristles (about twelve) at the level and in front of the anterior superior orbitals. Mesonotum in dorsal view quadrate, a little narrower and a little longer than head with eyes, surface (except the dark anterior stripe) shining, nearly flat, humeral calli moderately distinct, suture and postalar calli obsolete, depression in front of scutellum distinct but linear, bristles on each side are one moderate humeral, one very strong notopleural (more than half as long as width of mesonotum), two moderate postalars, a few sparse, irregularly placed microchaetes on each side in front; scutellum very small and transverse, three times as wide as long, with four widely spaced small bristles, each a little longer than length of scutellum; mesopleuron shining, meropleurite, metapleuron, and mediotergite very reduced, one moderate sternopleural (dEs2) bristle; wings represented by a narrow, sclerotized strip about as long as width of scutellum, bearing a few small bristles and a longer one at end; halteres absent. Legs with fore femora very thick, covered with rather sparse black bristles, a somewhat longer proximal ventral one and two or three postero-ventral ones a little longer, tibia with fine bristles and a longer, outstanding, dorsal, distal one, tarsi a little longer than tibia, basitarsus nearly as long as next two segments together; mid femur not thickened, besides the fine bristles with a stronger antero- and postero-dorsal one; mid tibia with an antero-ventral at $\frac{1}{2}$, an apical dorsal and five subequal apical ventrals, tarsus a little longer than the tibia, basitarsus a little longer than next two segments together, without strong bristles; hind femur not thickened, with a rather strong dorsal bristle at $\frac{4}{5}$, tibia with a distal dorsal bristle about twice as long as width of tibia and two short (not as long as width of tibia), rather stout, external apical spines, basitarsus not much enlarged for a member of the family, a little shorter than segment 2, with no distal spur. Abdomen very large, pyriform, posteriorly truncate, half as long again as broad, dorsal surface flattened (abdomen much flattened in profile), distinctly though not strongly constricted anteriorly, widest at middle of second tergal plate (= III), first tergal plate (= I + II) posteriorly nearly two-and-a-half times as wide as thorax, its median length a little greater than that of mesonotum, tergite III half as long as I + II but a little broader, IV almost the same size as III, V distinctly shorter and narrower, VI and VII visible as narrow crescents beneath the end of V, VI about two-thirds as wide as V; tergites II-V with moderately well marked off posterior margins, lateral margins sharp but not raised; sternites very broad, moderately sunk into the tergites, shining, with sparse pubescence; sternites VI and VII similar but very short; each cercus in the form of a small subtriangular plate with a small postero-internal knob bearing two long and two short, somewhat woolly bristles; tergites shining, with sparse microchaetes in two to three transverse rows.

FALKLAND ISLANDS: Kidney Island, from neck of the penguin *Eudyptes chrysocome nigrivestis* Gould (Rock-hopper Penguin), 10.iv.1936. Type ♀. Type in the collection of the British Museum.

It is not clear whether the above species is really an ectoparasite of the penguin.

The species is so modified as a result of the reduction of the wings that it is not easy to relate it to other Sphaerocerids, but I suspect from the nature of the bristles on the mid and hind tibiae that it is really a reduced member of the *Archiborborus* group. For this reason one pair of head bristles has been termed postocellars (these occur in *Archiborborus* as well as preocellars); the rather anterior position of this pair of bristles supports the view that they are not postverticals. It differs from all other described Sphaerocerids in its narrow, membraneless wings combined with the absence of halteres. Of the antarctic forms with reduced wings, *Antrops* Enderlein has oval wings at least as big as the scutellum and the halteres are present. *Anatalanta* Eaton is completely wingless. *Siphlopteryx* Enderlein has minute, scale-like wings and five long and two short dorsal bristles on mid tibia.



1. Dorsal view of *Penola eudyptidis* sp. n., legs omitted.

BRITISH MUSEUM (NATURAL HISTORY)

BRITISH GRAHAM LAND EXPEDITION

1934-37

SCIENTIFIC REPORTS

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TIDAL OBSERVATIONS IN
GRAHAM LAND

PART I

By BRIAN ROBERTS, M.A., Ph.D.

Scott Polar Research Institute, Cambridge

PART II

By R. H. CORKAN, M.Sc.

Liverpool Observatory and Tidal Institute

WITH FIVE TEXT FIGURES

LONDON

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TIDAL OBSERVATIONS IN GRAHAM LAND

(With five text figures)

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PART I by BRIAN ROBERTS, M.A., Ph.D.

THE TIDAL OBSERVATIONS OF THE BRITISH GRAHAM LAND EXPEDITION, 1934-37

DURING the British Graham Land Expedition, 1934-37, tidal observations were made at both base stations: in Stella Creek, Argentine Islands (lat. 65° 15' S., long. 64° 16' W.) during the period May 16th to December 27th 1935, and at Barry Island, one of the Debenham Islands in Marguerite Bay (lat. 68° 08' S., long. 67° 15' W.) during the period July 22nd to December 5th 1936.

There were considerable difficulties to be overcome in obtaining these records, and it has therefore seemed worth publishing a brief account of the two automatic gauges used. It must be understood that in both cases the design was limited by the material available, and that the observations had of necessity to be made in winter.

In the Argentine Islands the ship was firmly frozen into the ice in a narrow creek. Since there was no lateral movement with the tide, it was decided to use the up-and-down movement of the ship to work an instrument on deck where it would be easily accessible.

A flexible wire, made fast to a 40-lb. weight on the bottom of the sea A, passed through a guide pulley on a spar B, took a double turn round the drum of the instrument C, passed through guide pulleys D and E down to a counterbalance weight F and was secured to the end of the bearing-out spar (fig. 1). Where the wire passed through the ice, a short length of stove pipe was inserted and filled with fuel oil. The detail of the instrument is shown in fig. 2. The drum round which the operating wire passed was turned from a *lignum vitae* block sheave to $3\frac{1}{2}$ inches diameter and secured to a $\frac{1}{2}$ inch brass shaft, screwed 12 T.P.I. The guide pulley D was necessary to relieve the screw thread of excessive side strain when in the "up" position. A piece of $\frac{3}{16}$ inch brass wire, carrying the crosshead to work the pen, was recessed into the bottom of the brass shaft and kept up to its work by the spring of a hacksaw blade secured as shown. This wire was taken through a hole in the bottom of the box to steady the crosshead. The pen arm was pivoted on a wooden block secured to the side of the box and connected to the crosshead by a double link.

This gauge gave a scale reduction of 4 feet to 1.1 inches. It worked quite well, but had several disadvantages. The wires were exposed to wind and snow, and ice used to cause jamming and slipping. The top of the pipe through the ice was also exposed so that snow could get into the fuel oil. Eventually these difficulties were overcome by boxing in the whole of the wiring above the ice, but it became obvious that a better design would be necessary for use the second year. Changes in the ice round the ship, due to the weight of accumulated drift snow and to the loading and unloading of cargo, made it difficult to keep the datum of the observations constant.

As a result of the experience gained during the first winter, another gauge (fig. 3), was built for use in Marguerite Bay. The pen was operated by a rack driven off a worm and worm wheel which was taken from one of the ship's skylights. A pulley was attached to the end of the worm wheel spindle and grooved to take a length of trulay wire, one end of which was attached to a weight on the bottom of the sea and the other to a counterbalance weight. It so happened that the scale reduction worked out at exactly 1 foot to 1 centimetre (approximately 30 : 1). The gauge stood on a small table (fig. 4) on the sea-ice in front of the hut.

This instrument worked very satisfactorily for 5 months. The oil-filled pipe leading through the ice was 9 feet in length, having an inside diameter of 3 inches. It was arranged with its top end about 10 inches below the bottom of the instrument. Despite frequent heavy drifting, no trouble was caused by drift entering the pipe, and at no time was it necessary to put more oil into the pipe. In making another gauge of this type it would be more convenient to arrange the pulley over which the wire passes in such a way that the loop of wire can be put on and off without the necessity of threading it from one end. No difficulty was experienced with the counterpoise weight twisting round the other wire. The counterpoise weight must be long and thin so that it can be drawn up through the pipe, and the correct length of wire must be carefully calculated so that the counterpoise weight is as near as possible to the foot of the pipe at the highest tides. A bottom weight of at least 40 lb.,

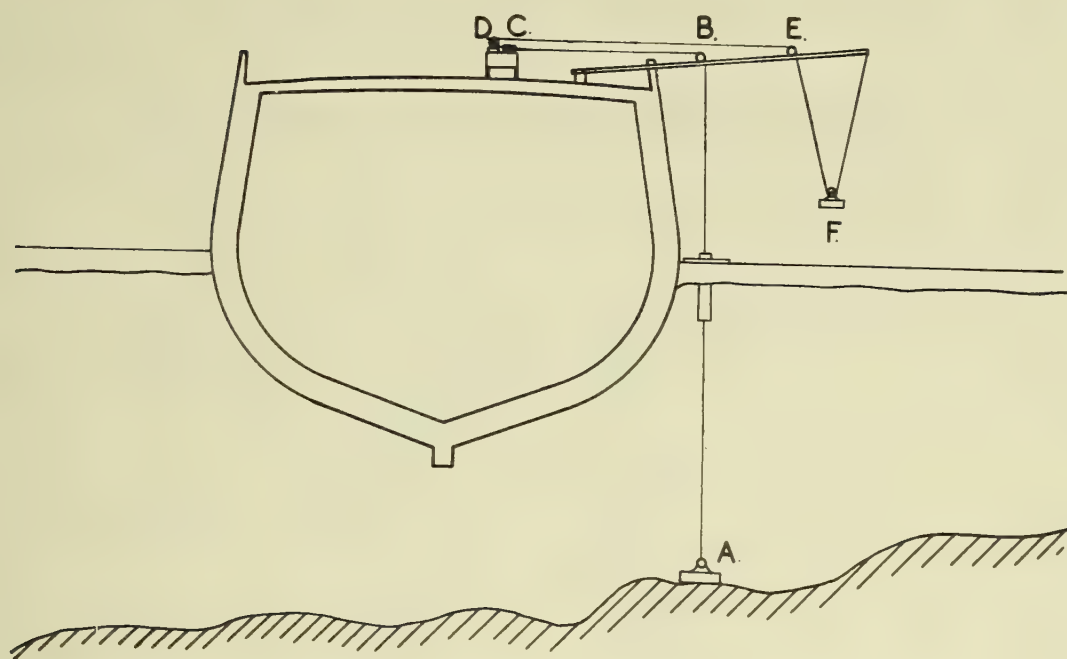


FIG. 1.

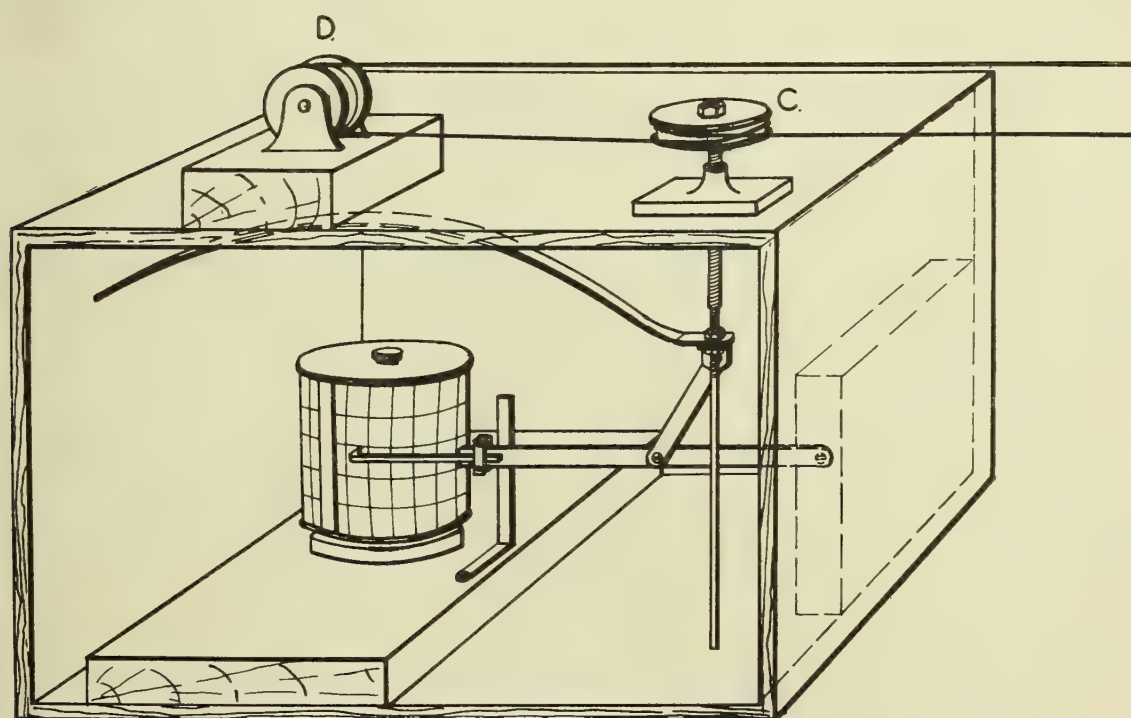


FIG. 2.

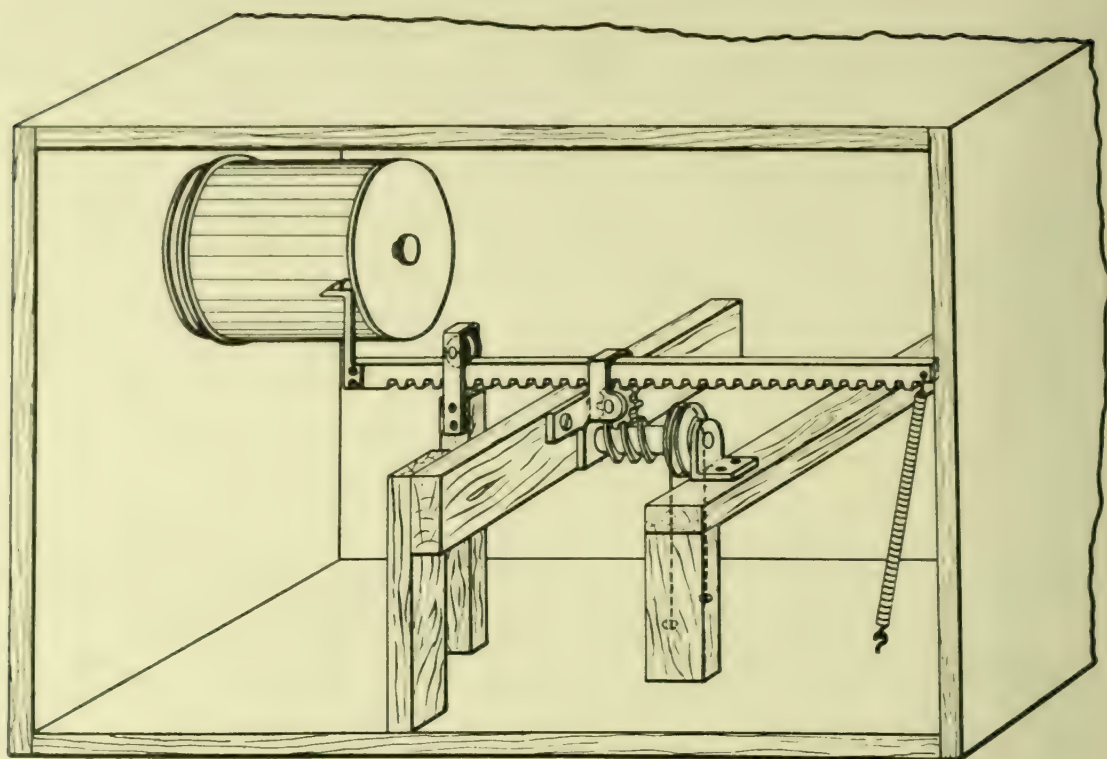


FIG. 3.

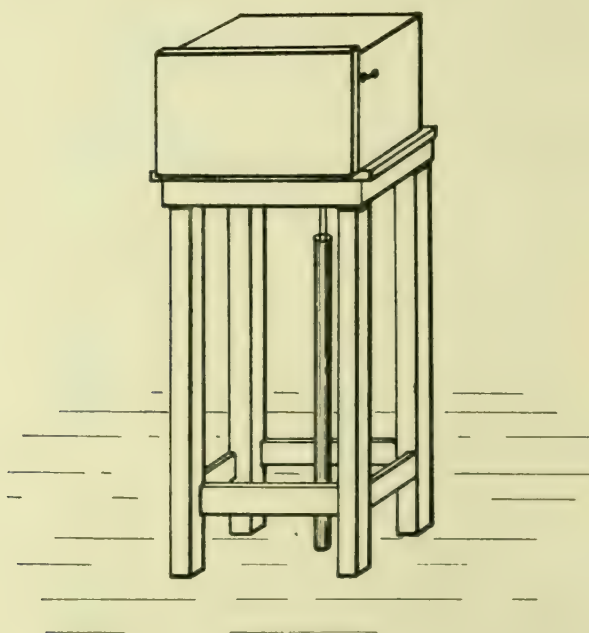


FIG. 4.

and a counterpoise of about 20 lb., proved satisfactory. The recording drums made 1 revolution in 1 week. Printed charts were not available and foolscap sheets were therefore cut to the required size (3.6×11.8 inches). It was, of course, necessary to use a special low temperature ink.

While the gauges were running, a time mark was put on the chart each morning as a check on the clock. This was made possible by the co-operation of Colin Bertram, who gave considerable assistance in 1935, and who was, in fact, entirely responsible for working the second gauge in Marguerite Bay. During his absence on a sledge journey, from September 4th to November 23rd 1936, this gauge was looked after by J. I. Moore. The writer also wishes to acknowledge much help from Lieutenant-Commander H. Millett, R.N., chief engineer of the Expedition, who was largely responsible for the construction of the first gauge.

PART II by R. H. CORKAN, M.Sc.

1. REDUCTION OF THE TIDAL OBSERVATIONS OF THE BRITISH GRAHAM LAND EXPEDITION, 1934-37

THE tidal observations taken by the British Graham Land Expedition, 1934-37, were forwarded to the Tidal Institute for analysis in January 1938.

The registrations were on foolscap sheets on which were marked the datum line and one time mark for each day. For the purpose of reading off the hourly heights, special scales were prepared on tracing paper from the constructional details given in the log book.

Two separate periods of 29 days were analysed for each of the two base stations, and the results are given in Table I. The amplitudes are in feet and the phase lags are referred to the Meridian of 60° West, in standard notation "g".

At Stella Creek special precautions were taken during the observations to keep the datum constant, by sighting on a vertical pole, marked off in feet and half feet, which was erected on the shore close to the ship. The pen was adjusted so that the central horizontal line on the chart corresponded to 5 feet on the pole. Due to slipping of the wire and other causes, on testing, the datum was frequently found to have changed, so that the values of mean sea-level can only be regarded as approximate.

At Barry Island, the datum was not referred to a fixed mark.

The consistency between the constants at each place from the separate monthly analyses is very satisfactory, especially when one considers the small scale of the registrations and the difficulties which had to be overcome.

2. REDUCTION OF THE TIDAL OBSERVATIONS OF THE EXPEDITION TO GRAHAM LAND, 1920-22

A general account of the expedition to Graham Land, 1920-22, has been given in the *Geographical Journal* for September 1923. Tidal observations were taken by

TABLE I
BRITISH GRAHAM LAND EXPEDITION, 1934-37
Harmonic Tidal Constants (Standard Time—4 hours West)

<i>Place, Position.</i>	<i>Central Day.</i>	<i>M₂</i> H. g.	<i>S₂</i> H. g.	<i>N₂</i> H. g.	<i>K₂</i> H. g.	<i>K₁</i> H. g.	<i>O₁</i> H. g.	<i>P₁</i> H. g.	<i>M₁</i> H. g.	<i>MS₁</i> H. g.	<i>Mean Sea Level</i>
Argentine Islands, Stella Creek 60° 15' S. 64° 16' W.	Sept. 13th 1935	0.79 174	0.68 275	0.14 20	0.18 275	1.28 25	1.09 14	0.42 25	0.04 297	0.03 48	4.64
	Dec. 6th 1935	0.82 181	0.68 268	0.11 33	0.18 268	1.17 28	1.08 13	0.39 28	0.03 297	0.05 114	5.40
Barry Island 68° 08' S. 67° 05' W.	Sept. 21st 1936	0.53 150	0.64 305	0.14 45	0.17 305	1.09 35	0.83 21	0.36 35	0.03 313	0.01 131	
	Oct. 27th 1936	0.48 150	0.63 299	0.23 47	0.17 299	1.07 32	0.79 14	0.35 32	0.02 331	0.02 205	

TABLE II
EXPEDITION TO GRAHAM LAND, 1920-22
Harmonic Tidal Constants

<i>Place, Position, Time kept.</i>	<i>Length.</i>	<i>Central Day.</i>	<i>M₂</i> H. g.	<i>S₂</i> H. g.	<i>N₂</i> H. g.	<i>K₁</i> H. g.	<i>O₁</i> H. g.
Water Boat Point* 64° 47' S. 62° 43' W. (Local Mean Time)	29 days	Nov. 30th 1921	0.89 168	0.69 244	0.06 89	1.05 12	0.99 4
Nansen Island (Svend Fogn Harbour) 64° 33' S. 61° 57' W. (Local Mean Time)	24 hours	Feb. 25th 1922	1.18 164	0.80 234	—	1.18 4	1.13 359
	24 hours	Feb. 26th 1922	1.18 163	0.80 233	—	1.25 22	1.20 16
	24 hours	Feb. 27th 1922	1.22 167	0.83 237	—	1.16 2	1.11 357
	2 days.†	[Feb. 25th & 27th 1922]†	1.29 167	0.78 238	—	1.20 6	1.08 359

* In *Admiralty Tide Tables*, Part II, 1932, p. 419, and in the *List of Harmonic Constants*, No. 2009, Special Publication No. 26 of the International Hydrographic Bureau, Monaco, the constants for Water Boat Point have been incorrectly published under the name "Lemaire Channel". The position given is correct, but unfortunately Lemaire Channel does not lie between Lemaire Island and the mainland where these observations were made. It is the name given to another channel about 70 miles to the south-west. The strait between Lemaire Island and the mainland has no name as yet.

† Combined by Elimination Method.

M. C. Lester and T. W. Bagshawe during their stay at their base, Water Boat Point, close to Andvord Bay, on the Danco Coast (lat. $64^{\circ} 47' S.$, long. $62^{\circ} 43' W.$), and later at Svend Foyn Harbour, Nansen Island (lat. $64^{\circ} 33' S.$, long. $61^{\circ} 57' W.$). At both stations, eye-readings were taken on a tide pole of local construction.

Hourly readings for complete days were available for Water Boat Point from October 31st to November 5th 1921, and from November 16th to December 16th 1921. At Nansen Island, only three complete days, February 5th to February 7th 1922, were available. A period of 29 days at Water Boat Point was analysed by Dr. Doodson at the Tidal Institute in 1925 and the harmonic constants are given in Table II. The constants for Nansen Island, also given in Table II, have been recently determined at the Tidal Institute, using the new Admiralty Method of Analysis.¹ In the daily analyses, it was assumed that certain relations between the constants at Nansen Island were intermediate in value between the respective relations at Deception Island and Water Boat Point, in a ratio determined by the distances apart of the stations. In the Elimination Method no assumptions have been made. The astronomical conditions on the two days which were combined in the Elimination Method were not very favourable to the method, but it will be noticed that the constants are in agreement with the daily determinations.

3. THE TIDES IN DRAKE STRAIT

Tidal information along the coasts of Graham Land is of much theoretical interest, since it provides data from which the progression of the tide in Drake Strait, the strait between Graham Land and South America, may be deduced.

Cotidal charts for this area were given by Harris in 1904 (*Coast and Geodetic Survey Report*, 1904, Appendix No. 5, Cotidal Lines of the World), but due to the small number of observations that were then available, the charts were almost entirely hypothetical.

In Table III, all the known tidal constants for stations on the coasts of Graham Land, and of the neighbouring islands, have been collected together; for ease of comparison of the constants, a uniform standard time has been used throughout. It will be seen that tidal stations are now well distributed over the Western Coast of Graham Land, and that the constants are all consistent. Due to the extreme southerly position of Barry Island, the observations taken by the recent expedition are of much value, but it would appear that so far as the tides are concerned there is very little to be gained from further observations taken along the western coast; observations taken on the north-east coast of Graham Land would, however, be of some interest.

¹ A. T. Doodson and H. D. Warburg, *Admiralty Tide Tables*, Part III.

The Admiralty Method of Analyses enables the determination of constants for the four principal tidal constituents from 24 hourly observations, provided the harmonic constants for a nearby station, or preferably several such stations, have already been well determined. Further, if two sets of 24 hourly observations are available for days when certain astronomical conditions are fulfilled, then the harmonic constants can be obtained using what is known as the "Elimination Method" without any assumptions. It is impossible to explain here the astronomical conditions that are necessary for good results, but in general, if the two days are nearly a week apart, and preferably the days of spring or neap tides, or if the ages of the moon on the two days differ by nearly seven or twenty-one days, then the astronomical conditions will be favourable to the method. Since the number of observations used is small, the accuracy of the constants will depend on the accuracy of the observations. Days when the tides are disturbed by meteorological conditions should be avoided.

TABLE III
ANTARCTIC—GRAHAM LAND

Harmonic Tidal Constants (Standard Time—4 hours West)

<i>Place, Position.</i>	<i>M₂</i> H. g.	<i>S₂</i> H. g.	<i>N₂</i> H. g.	<i>K₂</i> H. g.	<i>K₁</i> H. g.	<i>O₁</i> H. g.	<i>P₁</i> H. g.	<i>Authority.</i>
Scotia Bay, South Orkney Islands 60° 44' S. 44° 39' W.	1.52 146	0.91 167	0.30 130	0.25 167	0.48 0	0.56 348	0.16 0	F. J. Selby and J. de G. Hunter. <i>Scotia</i> Antarctic Exp., 1901-04
Port Foster, Deception Island. 62° 58' S. 60° 34' W.	1.44 178	0.65 223	— —	0.16 223	0.80 2	0.86 11	0.27 2	R. E. Godfrey. Second French Antarctic Exp. 1908-10
Nansen Island, de Gerlache Strait. 64° 33' S. 61° 57' W.	1.24 170	0.79 241	— —	— —	1.20 9	1.11 3	— —	M. C. Lester and T. W. Bagshawe. Expedition to Graham Land, 1920-22
Water Boat Point, Danco Coast. 64° 47' S. 62° 43' W.	0.89 173	0.69 249	0.06 94	— —	1.05 15	0.99 7	— —	M. C. Lester and T. W. Bagshawe. Expedition to Graham Land, 1920-22.
Port Charcot, Wandell Island. 65° 04' S. 64° 02' W.	0.73 175	0.63 263	0.14 178	0.17 263	1.04 11	1.00 10	0.34 11	A. Matha. French Antarctic Expedition, 1903-05
Port Circumcision, Peterman Island 65° 10' S. 64° 14' W.	0.67 173	0.55 274	0.11 40	0.15 269	1.03 25	0.95 24	0.33 25	R. E. Godfrey. Second French Antarctic Exp., 1908-10
Stella Creek, Argentine Islands. 65° 15' S. 64° 15' W.	0.81 177	0.68 271	0.13 27	0.18 271	1.23 27	1.09 13	0.41 27	Brian Roberts. British Graham Land Exp., 1934-37.
Barry Island, Debenham Islands. 68° 08' S. 67° 05' W.	0.51 150	0.63 302	0.19 46	0.17 302	1.08 33	0.81 17	0.35 33	Brian Roberts. British Graham Land Exp., 1934-37.

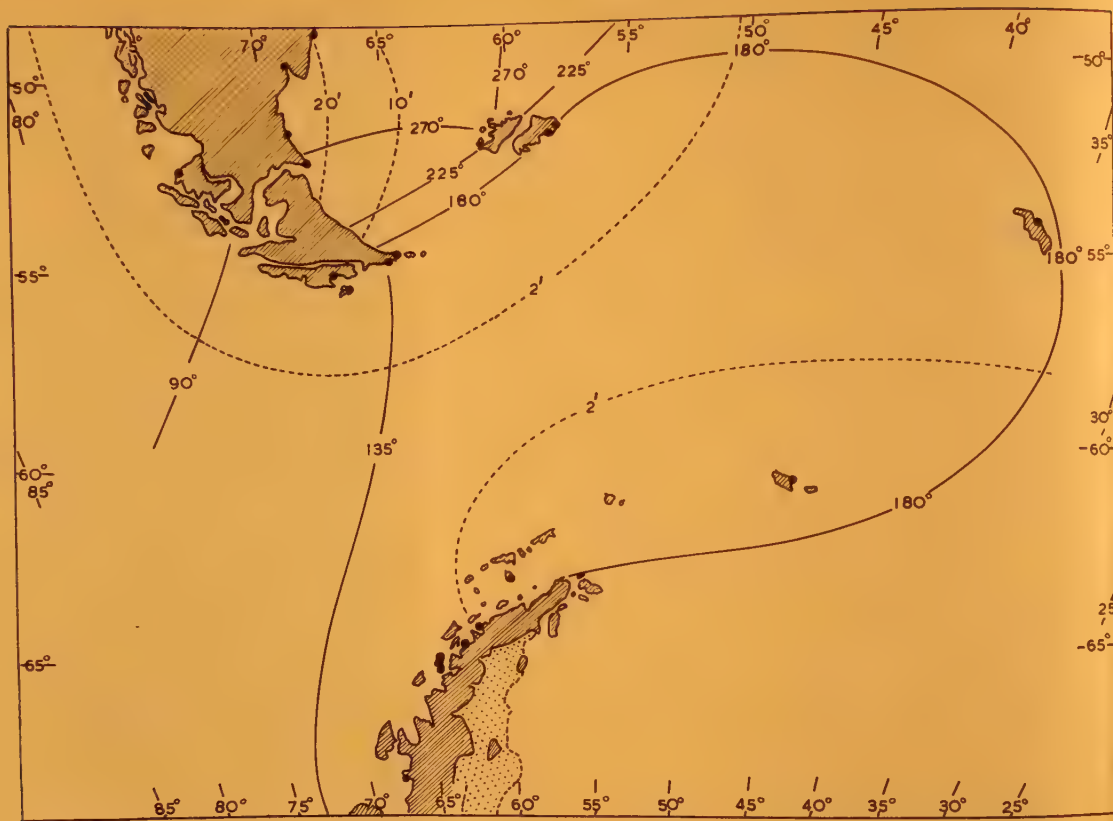


FIG. 5.—Cotidal and corange lines near Graham Land.

—— Cotidal lines.
 - - - - Corange lines.

Using the tidal constants for Graham Land, and also the tidal constants given in Admiralty Tide Tables (Part II), for all the stations marked in fig. 5, the cotidal and corange lines given in fig. 5 for the Principal Lunar Constituent (M) have been deduced.

The continuous lines join all places along which high water occurs at the same time. The lines have been deduced from interpolation in $H \cos g$ and $H \sin g$ of M_2 with Standard Time, 4 hours West. The lines drawn are those for which $g = 90^\circ, 135^\circ, 180^\circ, 225^\circ, 270^\circ$. These correspond to $g/30$ lunar hours, and $g/29$ solar hours after the transit of the moon over the meridian of 60°W . The Western Coast of Graham Land as far South as the Argentine Islands is very nearly a cotidal line.

The dotted lines in fig. 5 join all places having the same range of tide, and the figures give the range in feet.

The point at which the 2 feet corange lines emerges from the coast of Graham Land is intermediate between the stations at which observations were taken by the Expedition of 1920-22, and it has been fixed with some certainty.

The charts indicate that in the strait between Graham Land and South America there is a local progression of the time of high water from the Pacific to the Atlantic Oceans. At the Falkland Islands the tidal phenomena are divided into two parts; north-east of the Falklands, where the water is deep, the progression is rapid and turns to the North, but on the South-East coast, the progression is relatively slow.

On opposite sides of the strait, the progression is retarded on the coasts of South America and Graham Land to an almost identical extent. Thus, when in the centre of the strait, high water has advanced as far as South Georgia, on the coasts of Graham Land and South America high water occurs at their North-Eastern and South-Eastern extremities respectively.

The range of tide increases towards the South American and Antarctic Coasts and there is a tendency for an amphidromic point to be formed in the centre of the strait.

It might be stated here, for the attention of future explorers, that valuable information about the direction of cotidal and corange lines can be obtained from observations of tidal streams, taken either near the open coast or far out at sea. Preferably, and particularly when the tide is largely diurnal, as is the case in Graham Land, the observations should cover a continuous period of 24 hours and should include the speed and direction of the stream at hourly intervals. The general direction of the stream and the times of slack water are also of much value and may be obtained with relative ease. Lester and Bagshawe observed the current in the channel off Water Boat Point simultaneously, with their tidal observations, but owing to the enclosed position of their station and the fact that their observations were made in a channel where the currents were only partly of tidal origin, their observations are of very little use for our present purpose.

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1934-37

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*A BIBLIOGRAPHY
OF ANTARCTIC ORNITHOLOGY*

By

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Scott Polar Research Institute, Cambridge

WITH ONE TEXT FIGURE

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A BIBLIOGRAPHY OF ANTARCTIC ORNITHOLOGY

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(With one text-figure)

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INTRODUCTION

THESE notes have been prepared in the hope that future students of antarctic ornithology may be spared some of the labour of discovering what work has so far been accomplished in that Continent. After the British Graham Land Expedition of 1934–37, the writer started to prepare a summary of the present state of knowledge on the birds of the Antarctic. It soon became clear, however, that it is still too early to make the publication of such a work profitable. With the present taxonomic confusion, even the compilation of a list of species recorded from this interesting region presents serious difficulties. No adequate series of antarctic or sub-antarctic specimens, representing forms from the entire breeding range of a single genus, have yet been brought together; and if all existing collections were to be combined, they would still be quite inadequate for the purpose. Recent studies have revealed intricate diversity among certain groups, while others appear to have an extremely wide distribution without exhibiting any marked geographical variation. A sound classification of antarctic birds must await the collection of very many more specimens. Until this has been done, it is only possible to deprecate the confusion which is being still further increased by the repeated “juggling” of localities and sub-specific names.



FIG. 1.—The Antarctic and Sub-tropical convergences, and apparent mean position of the Ice-edge in Summer and Winter. From Data published in the *Discovery Reports*, by G. E. R. Deacon, N. A. Mackintosh, and H. F. P. Herdman.

This criticism, however, should not obscure the truth that taxonomy must be worked out to its practical limit before we can hope to interpret the subtler problems of distribution.

Much of the literature is difficult to trace, and it has, therefore, seemed worth collecting together all those references bearing on field work carried out within the antarctic regions. It is realized that the following bibliography is incomplete, but owing to the circumstances of the war, it has seemed best to publish it in its present form.

For the purposes of this summary, the geographical extent of the Antarctic is defined as all land and sea lying to the south of the Antarctic Convergence (see Fig. 1). That is to say, the region south of the line where the cold northward travelling antarctic surface water sinks beneath the warmer sub-antarctic water. It is a physical boundary very easily and precisely distinguished by the sudden change in water temperature between the two zones. The Antarctic Convergence probably forms the extreme northerly limit of pack-ice, but pack is rarely found so far north. There is already considerable evidence of its importance as a boundary in the distribution of marine life, and the relative zonal positions of the pan-antarctic islands are proving highly significant in relation to their respective avifaunas. The antarctic zone extends northwards to this Convergence, and includes some islands which have previously been considered from climatic reasons to be sub-antarctic.

Judged from this standpoint the Falkland Islands Dependencies are all antarctic, although the Falkland Islands themselves are sub-antarctic. Farther east, Bouvet Island, Heard Island and MacDonald Island are antarctic. Kerguelen lies just on the Convergence. Marion and Prince Edward Islands, and the Crozets, are just north of the Convergence, but so close to it that the cold antarctic surface water has not had time to sink far below the surface, and upwells against the obstructions. All these, therefore, come under the scope of this summary. Of the New Zealand sub-antarctic islands, Macquarie is included, but Auckland and Campbell lie too far north to be affected by the cold antarctic water. Cape Horn, the south Patagonian and Chilean coasts, Gough Island and Tristan da Cunha all fall within the sub-antarctic zone, and are not dealt with here.

Whilst admitting the inadequacy of this boundary from an ornithological point of view, it has seemed more satisfactory than the sixtieth parallel of latitude or the Antarctic Circle which have both been utilized previously, although neither can have any biological significance.

The area of the Continent has been computed at about five-and-a-half million square miles, or a region equal to the combined areas of Europe and Australia. The interior is almost entirely covered by a vast ice plateau devoid of life, and birds are restricted to the coasts and islands. The vast majority are found breeding on the oceanic islands lying for the most part hundreds of miles off-shore near the Antarctic Convergence. About seventy-five species have been recorded within this vast area.

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PART I

LIST OF ANTARCTIC EXPEDITIONS, WITH OBSERVERS
AND COLLABORATORS WHO HAVE PUBLISHED
ORNITHOLOGICAL RESULTS

THIS list aims to include the ornithological results of every antarctic expedition up to 1940. The general narratives of voyages have been included only when there are important bird references not covered by a separate report on birds. Many expeditions are omitted because no ornithological observations were published, but some of these brought home notes or specimens which were later described with other collections. Asterisks indicate authors who did not themselves take part in the expeditions. For published works, the dates in brackets are those of issue; for MSS. the dates of writing are similarly given in brackets but in italics. Some of the more important MSS. are included and their present locations are also indicated in the bibliography on pp. 347-360. Reviews are included only if they contain new information or corrections.

DATE	NATIONALITY, ETC.	LEADER	SHIP
1768-70	BRITISH EXPEDITION D. C. Solander (1768-70) ¹ S. Parkinson (1768-71) ²	James Cook	<i>Endeavour</i>
1772-75	BRITISH EXPEDITION W. Anderson (1772-75a, 1772-75b) ³ J. R. Forster (1781, 1785, 1844) G. Forster (1772-75, 1777) *M. H. C. Lichtenstein (1844) A. Sparrman (1785)	James Cook	<i>Resolution and Adventure</i>
1776-80	BRITISH EXPEDITION W. Anderson (1784) W. W. Ellis (1776-80)	James Cook	<i>Resolution and Discovery</i>
1819-21	RUSSIAN EXPEDITION ⁴ T. Bellingshausen (1831) *J. F. Brandt (1837a, 1837b) P. Mikhaylov (1831)	Thaddeus Bellingshausen	<i>Vostok and Mirnyi</i>
1820-23	BRITISH SEALING EXPEDITION TO PRINCE EDWARD AND CROZET ISLANDS C. M. Goodridge (1839)	William Veale	<i>Princess of Wales</i>
1822-24	BRITISH EXPEDITION J. Weddell (1825)	James Weddell	<i>Jane and Beaufoy</i>
1825-28	BRITISH SEALING EXPEDITION TO KERGUELEN ISLANDS *W. B. Clarke (1850) ⁵	—	<i>Royal Sovereign and Favorite</i>

¹ Copies of the original descriptions in the Solander MS. were published by Mathews (1912). These show that the first date on which a bird described from the Southern Ocean was procured was December 22, 1768. Iredale (1913) has summarized all that is known of Solander as an ornithologist.

² Parkinson's drawings were described by Salvin (1876).

³ Iredale (1938a) has recorded what is known of Anderson as an ornithologist.

⁴ The ornithological observations have been discussed by Roberts (1939). A translation of the Russian account of Macquarie Island is given by McNab (1909).

⁵ Based on information from J. Nunn.

DATE	NATIONALITY, ETC.	LEADER	SHIP
1828-30	BRITISH EXPEDITION W. H. B. Webster (1834)	Henry Foster	<i>Chanticleer</i>
1829-31	FIRST UNITED STATES EXPLORING EXPE- DITION J. Eights (1833) ¹ *E. Fanning (1834)	N. B. Palmer and B. Pendleton	<i>Annawan</i> and <i>Seraph</i>
1832-33	BRITISH SEALING EXPEDITION TO PRINCE EDWARD AND KERGUELEN ISLANDS *F. W. Hutton (1865) ²	—	—
1834(?)	SEALING EXPEDITION TO MACQUARIE ISLAND G. Bennett (1834)	—	—
1837-40	FRENCH EXPEDITION J. B. Hombron and C. H. Jacquinot (1841) J. Pucheran (1853)	J. Dumont d'Urville	<i>Astrolabe</i> and <i>Zélée</i>
1838-40	SECOND UNITED STATES EXPLORING EXPEDITION *J. Cassin (1858) T. R. Peale (1848a, 1848b) ³	Charles Wilkes	<i>Vincennes</i> , and five other vessels
1839-43	BRITISH ANTARCTIC EXPEDITION *H. S. Dove (1930) *H. O. Forbes (1899) G. R. Gray (1844) *G. R. Gray and *R. B. Sharpe (1844-76) ⁴ R. McCormick (1842, 1847, 1884)	James Clark Ross	<i>Erebus</i> and <i>Terror</i>
1851-53	AMERICAN WHALING AND SEALING EXPE- DITION TO KERGUELEN ISLANDS N. W. Taylor (1929)	E. Morgan	<i>Julius Cæsar</i>
c. 1860-70	SEALING EXPEDITIONS FROM CAPE-TOWN TO THE CROZET ISLANDS *F. Finn (1900) ⁵ *E. L. Layard (1867) ⁵	Captain Armson	—
1872-76	BRITISH EXPEDITION *W. A. Forbes (1882) H. N. Moseley (1879) *P. L. Sclater and *O. Salvin (1878) *M. Watson (1883) J. J. Wild (1878)	G. S. Nares	<i>Challenger</i>
1874-75	AMERICAN TRANSIT OF VENUS EXPEDITION TO KERGUELEN ISLANDS *E. Coues and J. H. Kidder (1875-76) *M. Lanen (1875)	—	<i>Swatara</i> and <i>Monongahela</i>
1874-75	BRITISH TRANSIT OF VENUS EXPEDITION TO KERGUELEN ISLANDS A. E. Eaton (1875) *R. B. Sharpe and *H. Saunders (1879) *A. Milne-Edwards (1879)	R. P. de Perry	<i>Volage</i> and <i>Supply</i>

¹ For information about Eights, see Calman (1937). A collection of bird skins was presented to the Boston Society of Natural History by J. N. Reynolds, who also took part in the Expedition. Eights' specimens and field notebooks have not been discovered. There are some interesting notes on the distribution of oceanic birds in the logbook of the schooner *Penguin*, a consort of the *Annawan*. This logbook is now in the Library of Congress.

² Partly based on observations by Richard Harris, R.N.

³ Discussed by Mathews (1929).

⁴ Discussed by Mathews (1930).

⁵ Notes on specimens collected by Capt. Armson.

DATE	NATIONALITY, ETC.	LEADER	SHIP
1874-76	GERMAN TRANSIT OF VENUS EXPEDITION TO KERGUELEN ISLANDS *J. Cabanis and A. Reichenow (1876) *—, Husker (1876) T. Studer (1876a, 1876b, 1879, 1889)	Captain von Schleinitz	<i>Gazelle</i>
1877	AMERICAN SEALING EXPEDITION TO SOUTH GEORGIA H. W. Klutschak (1881)	—	<i>Flying Fish</i>
1877	NEW ZEALAND WHALING AND SEALING EXPEDITION TO MACQUARIE ISLAND J. I. Thomson (1912?)	Captain Bezer	<i>Bencleugh</i>
1878-79	NEW ZEALAND SEALING EXPEDITION TO MACQUARIE ISLAND F. W. Hutton (1879)	—	—
1880-81	NEW ZEALAND SEALING EXPEDITION TO MACQUARIE ISLAND J. H. Scott (1882)	Captain Cowper	<i>Jessie Niccol</i>
1882-83	GERMAN INTERNATIONAL POLAR YEAR EXPEDITION TO SOUTH GEORGIA D. Pagenstecher (1885) K. v. de Steinen (1890) H. Will (1884) J. Cabanis (1884, 1888)	—	<i>Marie</i>
1885-86	AMERICAN SEALING EXPEDITION TO SOUTH GEORGIA *G. E. Verrill (1895) ¹	—	<i>Express</i>
1887-89	AMERICAN SEALING EXPEDITION TO GOUGH ISLAND, CROZETS, KERGUELEN, AND SOUTH GEORGIA *G. E. Verrill (1895) ¹	Captain Fuller	<i>Francis Allen</i>
1892-93	DUNDEE WHALING EXPEDITION W. S. Bruce (1894a, 1894b, 1894c) C. W. Donald (1894a, 1894b) *P. L. Selater (1894)	—	<i>Balaena, Active Diana and Polar Star</i>
1893-94	NORWEGIAN WHALING EXPEDITION C. A. Larsen (1894)	C. A. Larsen	<i>Jason</i>
1894	SEALING EXPEDITION FROM INVERCARGILL TO MACQUARIE ISLAND A. Hamilton (1894)	—	<i>Gratitude</i>
1894	AMERICAN SEALING EXPEDITION TO KER- GUELEN ISLANDS *R. G. Hazard (1894) ²	J. J. Fuller	<i>Francis Allen</i>
1895	NEW ZEALAND SEALING EXPEDITION TO MACQUARIE ISLAND W. H. Bickerton (1897) *A. J. Campbell (1901) ³	—	<i>Gratitude</i>
1897-98	SEALING EXPEDITION FROM MELBOURNE TO KERGUELEN ISLANDS R. Hall (1900, 1910)	H. Gundersen	<i>Edward</i>

¹ Notes on specimens collected by G. Comer, one of the sealers.

² Based on information from Capt. J. J. Fuller.

³ Notes on specimens collected by J. Burton, one of the sealers of the *Gratitude*, which made three voyages annually to Macquarie between about 1890 and 1895.

DATE	NATIONALITY, ETC.	LEADER	SHIP
1897-99	BELGIAN ANTARCTIC EXPEDITION ¹ E. G. Racovitza (1900, 1901) *H. Saunders (<i>n.d.</i>)	A. de Gerlache	<i>Belgica</i>
1898-99	GERMAN DEEP-SEA EXPEDITION C. Chun (1900) *M. Lewin (1902) *H. Männich (1902) *A. Reichenow (1904a, 1904b) *F. Ulrich (1904) E. Vanhöffen (1901)	C. Chun	<i>Valdivia</i>
1898-1900	BRITISH ANTARCTIC EXPEDITION L. C. Bernacchi (1901) *R. B. Sharpe (1902) N. Hanson (1902)	C. Borchgrevink	<i>Southern Cross</i>
1901-02	SWEDISH ANTARCTIC EXPEDITION *F. Ameghino (1906) K. A. Andersson (1905) E. Lönnberg (1905) *C. Wiman (1905)	O. Nordenskjöld	<i>Antarctic</i>
1901-03	GERMAN SOUTH POLAR EXPEDITION A. Reichenow (1908a, 1908b) E. Vanhöffen (1903, 1904, 1905, 1912a, 1912b) E. Werth (1925)	E. von Drygalski	<i>Gauss</i>
1901-04	BRITISH NATIONAL ANTARCTIC EXPE- DITION H. T. Ferrar (1928) *W. P. Pycraft (1907) E. A. Wilson (1901-03, 1901-04, 1905a, 1905b, 1905c, 1907)	R. F. Scott	<i>Discovery</i>
1902	LORD RANFURLEY'S EXPEDITION TO NEW ZEALAND SUB-ANTARCTIC ISLANDS *W. R. Ogilvie-Grant (1905)	—	<i>Tutanekai</i>
1902-04	SCOTTISH NATIONAL ANTARCTIC EXPEDI- TION W. S. Bruce (1907) W. S. Bruce and D. W. Wilton (1904) *W. E. Clarke (1906a, 1906b, 1907) *W. E. Clarke, L. N. G. Ramsey, R. N. Rudmose Brown, and W. S. Bruce (1913) *D. Waterston and *A. Campbell Geddes (1909) D. W. Wilton, J. H. Harvey Pirie and R. N. Rudmose Brown (1908)	W. S. Bruce	<i>Scotia</i>
1903-05	FIRST FRENCH ANTARCTIC EXPEDITION R. Anthony (1907) *R. Babin (1911) A. Ménégaux (1907, 1908) E. Turquet (1906)	J. B. Charcot	<i>Français</i>
1904-05	ARGENTINE METEOROLOGICAL STATION, SOUTH ORKNEY ISLANDS L. H. Valette (1906)	R. C. Mossman	—

¹ Three papers: "Bile des Oiseaux Antarctiques," by P. Portier, "Oiseaux (Biologie)" by E. G. Racovitza, and "Oiseaux (Systematique)" by Howard Saunders, were included in the printed list of proposed reports of this Expedition. None of these was published. The specimens were determined by Howard Saunders in the British Museum, and Monsieur Racovitza proposed to add his field notes. In April, 1938, however, this was still incomplete, and the *Commission de la Belgica* then requested Monsieur Charles Dupond to edit a report on the ornithological results of the Expedition. The report is still unpublished.

DATE	NATIONALITY, ETC.	LEADER	SHIP
1904-05	ERIK SÖRLING'S VOYAGE TO SOUTH GEORGIA *E. Lönnberg (1906)	—	—
1906	A. SZIELASKO'S VOYAGE TO SOUTH GEORGIA A. Szielasko (1907, 1924, 1926)	—	—
1907	NEW ZEALAND SUB-ANTARCTIC ISLAND EXPEDITION E. R. Waite (1909)	—	<i>Hinemoa</i>
1907-09	BRITISH ANTARCTIC EXPEDITION *R. A. Falla (1937) ¹ J. Murray (1909)	E. H. Shackleton	<i>Nimrod</i>
1908	NORWEGIAN WHALING EXPEDITION C. A. Larsen (1908)	C. A. Larsen	<i>Undine</i>
1908-10	SECOND FRENCH ANTARCTIC EXPEDITION *R. Anthony (1907) *R. Anthony and L. Gain (1912, 1913, 1915) *R. Babin (1911) L. Gain (1911, 1913a, 1914a, 1914b, 1928) *F. Haverschmidt (1934)	J. B. Charcot	<i>Pourquoi Pas?</i>
1910-13	BRITISH NATIONAL ANTARCTIC EXPEDITION A. Cherry-Garrard (1922) *P. R. Lowe and *N. B. Kinnear (1930) G. Murray Levick (1914, 1915) *C. W. Parsons (1934) H. L. L. Pennell (1911-13) R. E. Priestley (1911) *W. E. Shoults (1932) E. A. Wilson (1910a, 1910b, 1910-11) E. A. Wilson, E. H. Bowers and A. Cherry-Garrard (1913)	R. F. Scott	<i>Terra Nova</i>
1911-14	AUSTRALASIAN ANTARCTIC EXPEDITION G. F. Ainsworth (1915) *R. A. Falla (1937) ² D. Mawson (1915) *A. J. North (1913)	D. Mawson	<i>Aurora</i>
1912-13	BROOKLYN MUSEUM AND AMERICAN MUSEUM OF NATURAL HISTORY EXPEDITION TO SOUTH GEORGIA R. C. Murphy (1914a, 1914b, 1914c, 1915, 1916a, 1916b, 1916c, 1917, 1918a, 1918b, 1922, 1923, 1936a) R. C. Murphy and *F. Harper (1916) *J. T. Nichols and R. C. Murphy (1914) *R. U. Schufeldt (1914)	—	<i>Daisy</i>
1912-14	FRENCH EXPEDITION TO KERGUELEN ISLANDS J. Loranchet (1915-16)	R. R. du Baty	<i>Curieuse</i>
1914-16	BRITISH IMPERIAL TRANS-ANTARCTIC EX- PEDITION R. W. James (1916) F. A. Worsley (1914-16)	E. H. Shackleton	<i>Endurance</i>
1914-17	SHACKLETON'S ROSS SEA PARTY *R. A. Falla (1937) ³	A. Mackintosh	<i>Aurora</i>

¹ Field notes from D. Mawson.² Field notes from L. R. Blake, H. Hamilton, C. T. Harrison, J. G. Hunter, S. E. Jones, C. F. Laceron, D. Mawson and E. R. Waite.³ Field notes from A. H. Ninnis.

DATE	NATIONALITY, ETC.	LEADER	SHIP
1915	COMMONWEALTH METEOROLOGICAL EXPE- DITION TO MACQUARIE ISLAND *R. A. Falla (1937) ¹ A. Tulloch (1916)	A. Tulloch	—
1920-21	NORWEGIAN WHALING EXPEDITION TO SOUTH SHETLAND ISLANDS A. K. Neilsen (1921)	—	—
1920-22	BRITISH EXPEDITION TO GRAHAM LAND T. W. Bagshawe (1920-22, 1938, 1939)	—	—
1921-22	SHACKLETON-ROWETT EXPEDITION F. Wild (1923) G. H. Wilkins (1922, 1923)	E. H. Shackleton	<i>Quest</i>
1923-24	NORWEGIAN WHALING EXPEDITION A. J. Villiers (1925)	C. A. Larsen	<i>Sir James Clark Ross</i>
1924-25	FRENCH GOVERNMENT MISSION TO SOUTH- ERN OCEAN P. Idrac (1925)	—	—
1925-27	GERMAN ATLANTIC EXPEDITION E. Hentschel (1933)	A. Merz	<i>Meteor</i>
1925-27	DISCOVERY COMMITTEE'S INVESTIGATIONS AT SOUTH GEORGIA L. Harrison Matthews (1929, 1931)	—	—
1926-27	A. CARCELLES' VOYAGE TO SOUTH GEORGIA A. Carcelles (1927)	—	—
1927-28	NORWEGIAN ANTARCTIC EXPEDITION *B. Aagaard (1930-34) O. Olstad (1929)	H. Horntvedt	<i>Norvegia</i>
1928-29	NORWEGIAN ANTARCTIC EXPEDITION *B. Aagaard (1930-34) O. Olstad (1929)	Nils Larsen	<i>Norvegia</i>
1928-29	GERMAN SOUTH GEORGIA EXPEDITION L. Kohl-Larsen (1930)	L. Kohl-Larsen	—
1928-29	E. AUBERT DE LA RUE'S FIRST EXPEDITION TO KERGUELEN AND HEARD ISLANDS E. Aubert de la Rue (1930)	—	—
1928-30	FIRST BYRD ANTARCTIC EXPEDITION P. A. Siple (1931)	R. E. Byrd	<i>City of New York, and Eleanor Bolling</i>
1929-30	A. CARCELLES' VOYAGE TO SOUTH GEORGIA A. Carcelles (1931, 1932) ²	—	—
1929-31	DISCOVERY COMMITTEE'S INVESTIGATIONS: (FIRST COMMISSION) S. Kemp and A. L. Nelson (1931) *C. W. Parsons (1932)	S. Kemp	<i>Discovery II</i>
1929-31	B.A.N.Z. ANTARCTIC RESEARCH EXPEDITION *W. L. Crowther (1933) R. A. Falla (1937) *T. Iredale (1938b)	D. Mawson	<i>Discovery I</i>
1931	E. AUBERT DE LA RUE'S SECOND EXPE- DITION TO KERGUELEN ISLANDS E. Aubert de la Rue (1932)	—	—

¹ Field notes from A. Tulloch.² Collecting for Museo Nacional de Historia Natural, Buenos Aires.

DATE	NATIONALITY, ETC.	LEADER	SHIP
1931-33	DISCOVERY COMMITTEE'S INVESTIGATIONS (SECOND COMMISSION) R. A. B. Ardley (1936) *R. A. Falla (1936) *R. C. Murphy (1936b)	D. D. John	<i>Discovery II</i>
1933-35	DISCOVERY COMMITTEE'S INVESTIGATIONS (THIRD COMMISSION) T. J. Hart (1934-35)	N. A. Mackintosh	<i>Discovery II</i>
1933-35	SECOND BYRD ANTARCTIC EXPEDITION A. A. Lindsey and P. A. Siple (1937) P. A. Siple (1936)	R. E. Byrd	<i>Bear of Oakland and Jacob Ruppert</i>
1934-37	BRITISH GRAHAM LAND EXPEDITION B. Roberts (1934-37, 1940a, 1940b)	J. Rymill	<i>Penola</i>
1935-36	DISCOVERY COMMITTEE'S WHALE MARKING CRUISE IN SOUTHERN OCEAN G. W. Rayner (1940)	C. R. V. Boothby	<i>William Scoresby</i>
1935-37	DISCOVERY COMMITTEE'S INVESTIGATIONS (FOURTH COMMISSION) B. Roberts (1936) J. R. Strong (1936-37)	G. E. R. Deacon	<i>Discovery II</i>

ADDITIONAL NOTE

THE papers by A. G. Bennett were based on experience while serving as Whaling Magistrate in the South Shetlands (1913-14, 1917-19, 1921-23 and 1925-27), and in the South Orkneys (1914-15).

A. G. BENNETT (1920, 1926, 1927a, 1927b, 1931a, 1931b)

*J. H. FLEMING (1924)¹

J. E. Hamilton, Government Naturalist of the Falkland Islands, was seconded for service in the Discovery Committee's Investigations in 1924. He spent the following whaling seasons in the south, and was able to carry out some ornithological work: South Shetlands (1920-21, 1923-24), South Sandwich Seas (1927-28), and South Georgia (1926-28).

J. E. HAMILTON (1934).

¹ Based on specimens collected by A. G. Bennett.

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PART III

MISCELLANEOUS PUBLICATIONS BASED ON MUSEUM AND
LITERARY RESEARCH

THE following list includes publications which cannot be related to any particular expedition, and also a few works of a more general nature which should assist in tracing further references on morphology, taxonomy, and nomenclature.

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PART IV

INDEX OF LOCALITIES

SUMMARIES of the whole Antarctic avifauna have been produced by Sclater (1894), Schalow (1897), Martins (1900), Saunders (1901), Reichenow (1908), and Gain (1914).

The main references to special localities are listed below.

ROSS SEA REGION. (Long. 160° E. to 120° W.).

- | | |
|---|--|
| BERNACCHI, L. C. (1901). | MURRAY, J. (1909). |
| CHERRY GARRARD, A. (1922). | PENNELL, H. L. L. (1911). |
| FALLA, R. A. (1937). | PRIESTLEY, R. E. (1911). |
| FERRAR, H. T. (1928). | SHARPE, R. B. (1902). |
| GRAY, G. R., and SHARPE, R. B. (1844-76). | SHOULTS, W. E. (1932). |
| HANSON, N. (1902). | SIPLE, P. A. (1931, 1936). |
| LEVICK, G. M. (1914, 1915). | WILSON, E. A. (1901-03, 1901-04, 1905c, 1907, 1910b, 1910-11). |
| LINDSEY, A. A., and SIPLE, P. A. (1937). | WILSON, E. A., BOWERS, E. H., and CHERRY-GARRARD, A. (1913). |
| LOWE, P. R., and KINNEAR, N. B. (1930). | |
| MCCORMICK, R. (1842, 1847, 1884). | |

AUSTRALIAN ANTARCTIC TERRITORY AND ADÉLIE LAND. (Long. 45° E. to 160° E.).

- | | |
|--|-----------------------------------|
| CASSIN, J. (1858). | NORTH, A. J. (1913). |
| FALLA, R. A. (1937). | PEALE, T. R. (1848a). |
| HOMBRON, J. B., and JACQUINOT, C. H. (1841). | PUCHERAN, J. (1853). |
| MCCORMICK, R. (1842, 1847, 1884). | RAYNER, G. W. (1940). |
| MATHEWS, G. M. (1928). | REICHENOW, A. (1908a). |
| MAWSON, D. (1915). | VANHÖFFEN, E. (1903, 1904, 1905). |

GRAHAM LAND, SOUTH SHETLANDS, WEDDELL SEA AND BELLINGS-HAUSEN SEA. (Long. 20° W. to 120° W.).

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|--|--|
| ANDERSON, K. A. (1908). | LARSEN, C. A. (1894). |
| BABIN, R. (1911). | LÖNNBERG, E. (1905). |
| BAGSHAW, T. W. (1920-22, 1938, 1939). | MÉNÉGAUX, A. (1907). |
| BELLINGSHAUSEN, T. (1831). | MURPHY, R. C. (1916a, 1936a). |
| BENNETT, A. G. (1920, 1926, 1927a, 1927b, 1931a, 1931b). | NIELSEN, A. K. (1931). |
| BROWN, R. N. RUDMOSE (1908, 1913). | PEALE, T. R. (1848a). |
| BRUCE, W. S. (1894a, 1894b, 1907). | RACOVITZA, E. G. (1900, 1901). |
| BRUCE, W. S. and WILTON, D. W. (1904). | ROBERTS, B. (1934-37, 1936, 1939, 1940a, 1940b). |
| CALMAN, W. T. (1937). | ROTHSCHILD, <i>Lord</i> (1920). |
| CASSIN, J. (1858). | SAUNDERS, H. (<i>n.d.</i>). |
| DABBENE, R. (1921-26, 1922, 1923a). | SCLATER, P. L. (1894). |
| DONALD, C. W. (1849a, 1894b). | STRONG, J. R. (1936-37). |
| EIGHTS, J. (1833). | TURQUET, E. (1906). |
| FANNING, E. (1834). | WEBSTER, W. H. B. (1834). |
| FLEMING, J. H. (1924). | WILD, F. (1923). |
| GAIN, L. (1911, 1913a, 1914a, 1914b, 1928). | WILKINS, G. H. (1922, 1923). |
| HAMILTON, J. E. (1934). | WILTON, D. W., HARVIE PIRIE, J. H., and BROWN, R. N. RUDMOSE (1908). |
| HART, T. J. (1934-35). | WIMAN, C. (1905). |
| JAMES, R. W. (1914-16). | WORSLEY, F. A. (1914-16). |

PETER I. ISLAND.

AAGAARD, B. (1930-34).
 OLSTAD, O. (1929).

ROBERTS, B. (1939).

SOUTH GEORGIA.

ALLEN, H. T. (1920).
 ANDERSSON, K. A. (1908).
 ANDERSON, W. (1772-75b).
 BELLINGSHAUSEN, T. (1831).
 BENNETT, A. G. (1926).
 CABANIS, J. (1884, 1888).
 CARCELLES, A. (1927, 1931, 1932).
 DABBENE, R. (1921-26, 1923b).
 FORSTER, G. (1772-75, 1777).
 FORSTER, J. R. (1884).
 KOHL-LARSEN, L. (1930).
 LÖNNBERG, E. (1905, 1906).
 MATTHEWS, L. H. (1929, 1931).
 MURPHY, R. C. (1914a, 1915, 1916a, 1916b, 1917,
 1918b, 1922, 1923, 1936a).

MURPHY, R. C., and HARPER, F. (1916).
 NICHOLS, J. T., and MURPHY, R. C. (1914).
 PAGENSTECHEER, D. (1885).
 ROBERTS, B. (1934-37, 1936, 1939, 1940b).
 ROTHSCHILD, *Lord* (1920).
 SCHUFELDT, R. U. (1914).
 SPARRMAN, A. (1785).
 STEINEN, K. v. DE (1890).
 STRONG, J. R. (1936-37).
 SZIELASKO, A. (1907, 1924, 1926).
 VERRILL, G. E. (1895).
 WEDDELL, J. (1825).
 WILD, F. (1923).
 WILKINS, G. H. (1922, 1923).
 WILL, H. (1884).

SOUTH ORKNEY ISLANDS.

ARDLEY, R. A. B. (1936).
 BRUCE, W. S. (1907).
 BRUCE, W. S., and WILTON, D. W. (1904).
 CLARKE, W. E. (1906a, 1906b).
 CLARKE, W. E., RAMSEY, L. N. G., BROWN,
 R. N. RUDMOSE, and BRUCE, W. S. (1913).
 DABBENE, R. (1921-26).
 FALLA, R. A. (1936).

HOMBROU, J. B., and JACQUINOT, C. H. (1841).
 MURPHY, R. C. (1936a, 1936b).
 PUCHERAN, J. (1853).
 STRONG, J. R. (1936-37).
 VALETTE, L. J. (1906).
 WILTON, D. W., HARVIE PIRIE, J. H., and
 BROWN, R. N. RUDMOSE (1908).

SOUTH SANDWICH ISLANDS.

BELLINGSHAUSEN, T. (1831).
 KEMP, S., and NELSON, A. L. (1931).

LARSEN, C. A. (1908).
 MURPHY, R. C. (1936a).

BOUVET ISLAND.

AAGAARD, B. (1930-34).
 MURPHY, R. C. (1936a).

OLSTAD, O. (1929).
 REICHENOW, (1904a, 1904b).

MARION AND PRINCE EDWARD ISLANDS.

GOODRICH, C. M. (1839).
 HUTTON, F. W. (1865).

MOSELEY, H. N. (1879).
 WILD, J. J. (1878).

CROZET ISLANDS.

AUBERT DE LA RUE, E. (1930).
 BLYTH, E. (1860).
 FALLA, R. A. (1937).
 FINN, F. (1900).
 GOODRICH, C. M. (1839).
 LAYARD, E. L. (1867).

REICHENOW, A. (1904b, 1908a, 1908b).
 SHARPE, R. B. (1895-96).
 SOEUF, D. LE (1902).
 VANHÖFFEN, E. (1912b).
 VERRILL, G. E. (1895).

KERGUELEN ISLANDS.

- ANDERSON, W. (1772-75a, 1784).
 ANONYMOUS (1925).
 AUBERT DE LA RUE, E. (1930, 1932).
 CABANIS, J., and REICHENOW, A. (1876).
 CAMPBELL, A. J. (1927).
 CHUN, C. (1900).
 CLARKE, W. B. (1850).
 COUES, E., and KIDDER, J. H. (1875-76).
 EATON, A. E. (1875).
 ELLIS, W. W. (1776-80).
 GRAY, G. R., and SHARPE, R. B. (1844-76).
 HALL, R. (1900, 1910).
 HAZARD, R. G. (1894).
 HUSKER, —. (1876).
 HUTTON, F. W. (1865).
 LANEN, M. (1875).
 LORANCHET, I. (1915-16).
 MATHEWS, G. M. (1913, 1937b).
 MCCORMICK, R. (1842, 1847, 1884).
 MÉNÉGAUX, A. (1917).
 MILNE-EDWARDS, A. (1879).
 MOSELEY, H. N. (1897).
 REICHENOW, A. (1904a, 1904b, 1908a, 1908b).
 SCLATER, P. L., and SALVIN, O. (1878).
 SHARPE, R. B. (1875).
 SHARPE, R. B., and SAUNDERS, H. (1879).
 STUDER, T. (1876b, 1879, 1889).
 TAYLOR, N. W. (1929).
 ULRICH, F. (1904).
 VANHÖFFEN, E. (1901, 1903, 1904, 1905).
 VERRILL, G. E. (1895).
 WERTH, E. (1925).
 WILD, J. J. (1878).

HEARD ISLAND.

- FALLA, R. A. (1937).
 MOSELEY, H. N. (1879).
 REICHENOW, A. (1908a, 1908b).
 SCLATER, P. L., and SALVIN, O. (1878).
 VANHÖFFEN, E. (1912a).
 WILD, J. J. (1878).

MACQUARIE ISLAND.

- AINSWORTH, G. F. (1915).
 BELLINGSHAUSEN, T. (1831).
 BENNETT, G. (1834).
 BICKERTON, W. H. (1897).
 BRANDT, J. F. (1837b).
 BRYANT, C. E. (1933).
 CAMPBELL, A. J. (1901).
 CASSIN, J. (1858).
 CROWTHER, W. L. (1933).
 FALLA, R. A. (1937).
 HAMILTON, A. (1894).
 HUTTON, F. W. (1879).
 MATHEWS, G. M. (1935a, 1937c).
 MATHEWS, G. M., and IREDALE, T. (1935b).
 McNAB, R. (1909).
 MAWSON, D. (1915).
 MIKHAYLOV, P. (1831).
 MURRAY, J. (1909).
 OGILVIE-GRANT, W. R. (1905).
 OLIVER, W. R. B. (1930).
 PEALE, T. R. (1848a, 1848b).
 RAINE, T. (1822).
 ROBERTS, B. (1939).
 SCOTT, J. H. (1882).
 THOMSON, J. I. (1912?).
 TULLOCH, A. (1916).
 VILLIERS, A. J. (1895).
 WAITE, E. R. (1909).
 WILSON, E. A. (1901-03, 1901-04, 1907).

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